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THE ROLE OF ENVIRONMENTAL AND PHYSIOLOGICAL FACTORS IN THE SEASONAL CYCLE OF FATTY ACID COMPOSITION IN FEMALE NORTHERN PIKE (*Esox lucius* L.)

BY

©

KARL SCHWALME

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN
PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF:
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DEPARTMENT OF ZOOLOGY
EDMONTON, ALBERTA
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Abstract

Despite extensive laboratory research on factors influencing the fatty acid composition of animal tissues, the magnitude of changes in the fatty acid composition of natural fish populations and the role of environmental and physiological factors in these changes are unknown. This thesis reports the timing and magnitude of seasonal changes in the fatty acid composition of neutral lipid (NL) and polar lipid (PL) fractions of ovaries, liver, white muscle, and adipopancreatic tissue of female northern pike in Lac Ste. Anne, Alberta. Additional field collections and laboratory experiments were performed to assess the roles of ovarian recrudescence, diet, and temperature in these seasonal changes.

From late summer to winter, the PLs of all tissues exhibited significant declines in the weight percentage of saturated fatty acids which were compensated for by increases in monounsaturated fatty acids (MUFAs), n-3 polyunsaturated fatty acids (PUFAs), or both depending on the tissue. Liver was the only tissue to exhibit declines in the percentage of n-3 PUFAs in PLs during winter. The NLs of all tissues examined exhibited increases in the percentage of MUFAs and decreases in n-3 PUFAs during early winter. This may reflect an attempt to conserve dietary n-3 PUFAs for incorporation into the large quantities of PLs which accumulate in the ovaries, and to a lesser extent, in the somatic tissues of pike during early winter.

The content of neutral lipid fatty acids in liver of pike decreased greatly during late summer and fall and may have been due to reduced food intake associated with decreasing water temperatures. Increases in the PLFA content of white muscle and increased unsaturation of liver and muscle PLs during fall and winter also appeared to be primarily due to cold acclimation rather than to ovarian recrudescence. Increases in liver weight, liver PLFA content, and changes in the fatty acid composition of liver NLs during early winter were associated with both ovarian recrudescence and cold acclimation.

The fatty acid composition of the major lipid depots of pike, including the percentage of individual long chain PUFAs, was approximately the same as that of dietary lipids. This suggests that pike, like other strict carnivores, may have a dietary requirement for specific long chain PUFAs such as 20:4n6, 20:5n3, and 22:6n3. Accordingly, changes in dietary intake of individual n-3 and n-6 PUFAs may influence the fatty acid composition of pike lipids.

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List of Abbreviations used in this Thesis

Abbreviation	Definition
NL	neutral lipids
PL	polar lipids
TL	total lipids (ie: neutral and polar lipids combined)
NLFA	neutral lipid fatty acids (refers collectively to all types of fatty acids that occur as part of neutral lipids)
PLFA	polar lipid fatty acids (refers collectively to all types of fatty acids that occur as part of polar lipids)
EFA	essential fatty acids
SFA	saturated fatty acids
MUFA	monounsaturated fatty acids
PUFA	polyunsaturated fatty acids
n-3,n-6	indicates classes of fatty acids characterized as having the terminal double bond located three or six carbon atoms from the methyl end
AP tissue	adipopancreatic tissue
ANOVA	analysis of variance
SD	sample standard deviation
SE	standard error of the sample mean

Chapter I

General Introduction

Despite much research on the fatty acid metabolism of fish (see reviews by Henderson and Tocher 1987; Sargent et al. 1989; Hazel 1989), the effects of different environmental and physiological factors on the fatty acid composition of fish in natural populations remains unknown. Because many factors such as the reproductive cycle, diet, and temperature display a seasonal rhythmicity, their influence on fish fatty acid composition can be evaluated by examining the extent of seasonal changes in the fatty acid composition of fish lipids. Seasonal changes in fatty acid composition have been studied in marine fish such as mackerel (Hardy and Keay 1972), sprats (Hardy and Mackie 1969), cod (Jangaard et al. 1967), capelin (Henderson et al. 1984), anchovy (Yuneva et al. 1987), and herring (Henderson and Almatar 1989) and in a few freshwater fish such as perch and vendace (Agren et al. 1987) and juvenile atlantic salmon (Bergstrom 1989). However, none of the previous studies of seasonal changes in fatty acid composition were intended or detailed enough to differentiate between the effects of different environmental and physiological factors on fatty acid composition. Most of these studies examined the fatty acid composition of total lipids (Jangaard et al. 1967; Hardy and Mackie 1969; Henderson et al. 1984; Agren et al. 1987; Bergstrom 1989). Consequently it is not known if the seasonal changes in fatty acid composition in these studies are due to changes in the proportions of neutral lipid (NL) energy reserves and membrane polar lipids (PLs) (polyunsaturated fatty acids are more abundant in PL than in NL) or to changes in the fatty acid composition of these lipid fractions. In several cases fish were sampled at only two or three times of year (Hardy and Keay 1972; Dutta et al. 1985; Agren et al. 1987), and lipids were extracted from the whole body (Hardy and Mackie 1969) or from only one or two compartments (Henderson et al. 1984; Dutta et al. 1985; Agren et al. 1987; Yuneva et al. 1987; Henderson and Almatar 1989). The most serious limitations of previous studies are a lack of statistical rigor and lack of supporting experimental data designed to separate the relative contributions of individual environmental and physiological factors to the seasonal fatty acid cycles. Therefore, insight into the role of gonadal recrudescence, diet, and temperature in seasonal fatty acid cycles of fish must be obtained from other types of studies.

In many north-temperate fish, the annual reproductive cycle involves a large accumulation of lipid in the recrudescing ovaries (which may comprise up to 25 % of total body weight) and hence may have a marked effect on the total and relative quantities of fatty acids in somatic tissues (Henderson and Tocher 1987). Such an effect is suggested by the well defined reciprocal cycles in somatic and ovarian lipid content which occur in many north-temperate fish and which imply that a bulk transfer of lipids (and fatty acids) from somatic to ovarian tissues occurs seasonally (Newsome and Leduc 1975; Henderson et al. 1984; Nelson and McPherson 1986; Henderson and Almatar 1989). Selective transfer of PUFA from somatic to ovarian tissues may also occur because oocyte lipids of many north-temperate fish consist predominantly of PLs which are rich in PUFA (Kaitaranta and Ackman 1981; Tocher and Sargent 1984; Tocher et al. 1985; Falk-Petersen et al. 1986). In most north-temperate fish, the amount of lipid which accumulates seasonally in the recrudescing ovaries exceeds that in the male gonads by at least ten fold (Henderson and Tocher 1987). Therefore, females are the gender of choice with which to evaluate the influence of reproduction on the tissue fatty acid composition of fish.

Studies of fish nutrition have shown that the fatty acid composition of the diet can greatly influence the fatty acid composition of fish tissues. This is especially true of n-3 and n-6 PUFAs because these fatty acids fulfill essential physiological functions, yet cannot be synthesized by vertebrate animals, including fish, and are therefore required in the diet at certain minimum levels to prevent deficiency symptoms. Rainbow trout require omega-3 PUFAs in their diety at about 2.7 % of total calories in rainbow trout to prevent deficiency symptoms (Watanabe 1982; Bell et al. 1986). Omega-6 fatty acids appear to be essential dietary nutrients in warm water species such as tilapia and channel catfish and possibly in cold water species as well

(Castell 1979; Stickney et al. 1983). Accordingly, low percentages of either omega-3 or omega-6 PUFAs in the diet will decrease levels of the deficient fatty acids in tissues of fish and increase the proportions of other essential fatty acids (if available) and omega-9 unsaturated fatty acids in a compensatory manner (Castell et al. 1972b; Yu and Sinnhuber 1975). Additionally, studies by Bell et al. (1989) and Sowizral et al. (1990) have shown that the fatty acid composition of fish NLs and PLs can be influenced by changes in dietary fatty acid composition even when all experimental diets are replete in essential fatty acids.

The ability of fish to physiologically regulate tissue fatty acid composition appears to vary considerably between species. Fish such as freshwater salmonids which feed heavily on insects contain percentages of long chain PUFAs, notably 22:6n3 (30 % of total fatty acids), which are much higher than that of their diet (insects contain only trace amounts of 22:6n3; Hanson et al. 1985). Thus, freshwater salmonids have considerable capacity to regulate tissue fatty acid composition independently of diet composition and this appears to result from their comparatively good abilities to elongate and desaturate dietary fatty acids (Castell et al. 1972b; Hagve et al. 1986). Many marine fish, and possibly most piscivorous fish, have limited abilities to elongate and desaturate dietary fatty acids and therefore require specific long chain PUFAs such as 20:5n3 and 20:6n3 in their diet (Owen et al. 1972,1975; Bell et al. 1985a,b).

Therefore, dietary fatty acid composition may have a greater influence on tissue fatty acid composition in piscivorous fish than in invertebrate feeding ones.

The role of fatty acids in homeoviscous adaptation of cellular membranes has been well studied in north-temperate fish because, unlike most other vertebrates, these fish remain active over a wide range of body temperatures (Cossins and Prosser 1978; Hazel 1989). The influence of temperature on the fatty acid composition of total tissue polar lipids and polar lipids of individual membranes has been examined in many fish species and tissues and in several types of membranes (Caldwell and Vernberg 1970; Kemp and Smith 1970; Hazel 1979; Cossins and Prosser 1982; Avrova 1984; Christiansen 1984; Bly et al. 1986; Carey and Hazel 1989). In almost every instance, acclimation to low temperature increased the proportion of unsaturated fatty acids in the polar lipid fraction studied. The relative contribution of different monounsaturated and polyunsaturated fatty acids to the increased unsaturation at low temperatures varied with the species, tissue, and membrane type. In fish, the only membranes which have not been found to contain increased proportions of unsaturated fatty acids in response to cold acclimation are the mitochondrial membranes in red muscle of Carp (Wodtke 1981) and sarcoplasmic reticulum membranes in white muscle of goldfish (Cossins et al. 1978). Adjustments in membrane fatty acid composition reach completion in several days during warm acclimation and within about two weeks during cold acclimation (Cossins et al. 1977; Sellner and Hazel 1982a; Hagar and Hazel 1985). The biochemical mechanisms which regulate temperature related adjustments in polar lipid fatty acid composition in laboratory fish have been extensively studied (Hazel and Prosser 1979; Hazel and Neas 1982; Sellner and Hazel 1982a,b; Hazel 1983,1984,1989,1990). However, because fish in natural populations experience seasonal cycles in not only temperature but also dietary composition and gonadal recrudescence, it is important to determine whether they accomplish homeoviscous adaptation with the same changes in membrane fatty acid composition, and over similar time spans, as fish do under laboratory conditions.

The purpose of this thesis is to describe the timing and magnitude of seasonal cycles in the tissue fatty acid content of female northern pike (Esox Lucius L.) and thereby answer the following questions:

1) Are significant quantities of fatty acids transferred from somatic to ovarian tissues or from NLs to PLs during ovarian recrudescence ?

2) Are n-3 and n-6 essential fatty acids diverted away from somatic NLs during fall and early winter and thereby conserved for use in ovarian construction and PL restructuring ?

3) Does diet fatty acid composition appear to influence the whole body fatty acid composition of female pike ?

4) Are seasonal changes in the PL fatty acid composition of pike consistent with laboratory data on the effects of temperature on membrane fatty acid composition ?

Northern pike were chosen for this study because they possess several characteristics which make them good representatives of north-temperate fresh water fish in which to examine the role of environmental and physiological factors in seasonal fatty acid cycles. Pike are one of the few fresh water fish that have a circumpolar distribution and occur over a wide range of latitudes (Scott and Crossman 1973) and thus appear to be adapted to a wide range of environments. Among north-temperate fresh water fish, pike are neither the most cold-water adapted nor the most warm-water adapted, but are best described as cool-water adapted (Casselman 1978). Finally, female pike undergo large and well defined seasonal cycles of gonad recrudescence, body temperature, and food intake, but migrational movements and changes in dietary composition are minimal compared to most other fresh water fish (Diana 1979,1980). Therefore, the range of seasonally variable environmental and physiological factors which pike experience are somewhat restricted, making it easier to assess the relative influence of those factors which do exist.

In this thesis, chapters II and III describe the seasonal cycles which occur in the total and relative quantities of fatty acids in the major lipid depots of female pike and provide tentative explanations for these cycles. Chapters IV to VI report the results of endeavours designed to further clarify the roles of ovarian recrudescence, diet, and temperature in seasonal fatty acid cycles of pike. In chapter IV, the role of ovarian recrudescence in seasonal fatty acid cycles of pike somatic tissues is examined by comparing the fatty acid compositions of mature females which either were or were not undergoing ovarian recrudescence in Campbell Lake, Northwest Territories. The role of dietary fatty acid composition was assessed by comparing the fatty acid composition of female pike with that of their diet and is the subject of chapter V. Chapter VI describes the results of a controlled laboratory experiment designed to determine the influence of temperature acclimation on the fatty acid composition of pike liver and white muscle.

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Chapter II

Seasonal changes in the total neutral and polar lipid fatty acid content of female northern pike (Esox lucius L.) *

Introduction

In many north-temperate fish, ovarian growth occurs over winter as food intake becomes greatly reduced (Shul'man 1974; Love 1980). This suggests that somatic tissues may provide lipids and other nutrients for deposition into the maturing ovaries. It is important to evaluate the possibility of seasonal lipid transfers between body compartments of fish because such transfers would require appropriate enzymic, hormonal, and lipid transport adaptations.

Although lipid transfers from somatic to ovarian tissues have been estimated from reciprocal seasonal changes in the total lipid content of these tissues (Nelson and McPherson 1986; Tanasichuk and Mackay 1989), such transfers can be quantified more accurately from changes in tissue fatty acid content. Lipid transfers estimated from changes in the total weight of lipid in somatic and ovarian tissues do not account for changes in lipid weight which would occur (due to addition of polar head groups) if neutral lipids (NLs) were converted to polar lipids (PLs), or vice versa, during the transfer.

Several considerations suggest that lipids or fatty acids may be transferred seasonally, not only from somatic

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to ovarian tissues, but also from NL to PL compartments. For example, somatic lipid reserves consist predominantly of NLs whereas the ovarian lipids of many north-temperate fish are predominantly PLs (60 to 80 % of total lipid weight) (Kaitaranta and Ackman 1981; Tocher and Sargent 1984). Additionally, cold acclimation in fish appears to increase the abundance of mitochondrial (Tyler and Sidell 1984) and sarcoplasmic reticulum (Penny and Goldspink 1980) membranes in muscle which may in turn increase PL concentrations in this tissue. If north-temperate fish accumulate significant amounts of PLs in their ovaries and muscle over winter, and concurrently deplete NLs from somatic tissues, then seasonal transfers of fatty acids may occur between NLs and PLs. A few studies have examined seasonal changes in the NL and PL content of fish such as cod (Shatunovskiy 1971), scorpionfish (Shchepkin 1971), and mackerel (Hardy and Keay 1972), but because of small sample size, and few sampling periods and tissues examined, transfers of fatty acids between NLs and PLs could not be quantified.

The purpose of the present study was to measure seasonal changes in the NL fatty acid (NLFA) and PL fatty acid (PLFA) content of the major lipid depots in the northern pike (Esox lucius L.) and thereby estimate the quantity of fatty acids which might be transferred seasonally between somatic and ovarian tissues and between NLs and PLs.

Materials and Methods

Fish Collection

Five to eight adult female pike were collected using gill nets from Lac Ste. Anne, Alberta (53°, 42′ N, 114°, 22′ W) during each of ten collection periods between May 1987 and August 1988. In total, 68 pike were sampled. Their mean body weight and standard length were 944 g (SD=271) and 45.6 cm (SD=4.6) respectively. Pike were selected for analysis so as to minimize variation in standard length between and within samples. The ten samples of pike did not differ significantly in either average body weight or average standard length (one-way ANOVA, $P< 0.05$).

Gill nets were set for 1 to 2 h from May to September and for 14 to 16 h (overnight) during winter collections in January and March. Pike were stored in a freezer (-20°C) prior to lipid extraction from tissues which was usually completed within 6 h after removal of fish from the nets.

Lipid extraction and fatty acid analysis

Two grams each of ovary, liver, adipopancreatic (AP) tissue, and white muscle were excised from each fish. In pike, adipose tissue is intimately interspersed with pancreatic tissue (Plantikow et al. 1986) and is present exclusively as long strips of adipopancreatic tissue attached to the digestive tract. White muscle samples were excised as a 3 cm long strip taken from immediately in front of the dorsal fin and did not include red muscle fibres. Red muscle comprises less than 4 % of pike body wt (Schwalme and Mackay 1985) and thus is not a major lipid depot.

Chloroform and methanol were redistilled in glass prior to use to remove peroxides and trace contaminants. Lipids were extracted by homogenizing 2 g of tissue in 40 ml of a 2:1 mixture of chloroform/methanol (Folch et al. 1957) which contained antioxidant (butylated hydroxytoluene) at concentrations of at least 0.1 % of the total lipid content of the extract (Johnson 1971). After homogenization, chloroform/methanol extracts were filtered, bubbled with nitrogen to remove oxygen, and stored in completely filled, sealed glass vials at - 30°C until further preparation. Nonlipids were removed from the chloroform/methanol extract with the washing procedure (using 0.58 % NaCl solution) described by Folch et al. (1957). The lower phase resulting from the washing procedure received a known weight of tri-O-tridecanoylglycerol to supply tridecanoic acid (13:0) (after saponification) as an internal standard for quantifying the fatty acid content of neutral lipids. Solvents in the lower phase were then evaporated in a nitrogen atmosphere under reduced pressure and the remaining lipids dissolved in a small quantity of chloroform and applied to a column of silicic acid (mesh size 100-200). Neutral lipids and internal standard were eluted with 30 column volumes of chloroform and polar lipids were subsequently eluted with 30 column volumes of methanol (Rouser et al. 1967). A known weight of tri-O-tridecanoylglycerol was added to the methanol eluate as an internal standard for quantifying fatty acids in the polar lipid fraction. Recoveries of purified NL (tri-O-hexadecanoylglycerol) and PL (1,2-dieicosanoyl-sn-glycerol-3-phosphocholine) through silicic acid chromatography averaged 96.4 ± 4.9 % and 93.0 ± 2.0 % (means ± SD, n=5) respectively and cross contamination between the two lipid fractions was negligible. Since recoveries of NLs and PLs were similar, addition of internal standards at two different points in the protocol does not create problems in comparing levels of NLFAs and PLFAs.

Saponification and methylation of lipids was performed using the procedure of Bannon et al. (1982); the only modification being that lipids dissolved in 0.5 molar KOH in methanol were heated for one hour (instead of 15 min) and, subsequent to addition of 14 % boron trifluoride in methanol, heated for an additional 30 min.

The resulting fatty acid methyl esters were dissolved in iso-octane and quantified by gas chromatography using a 1.8 m long, 6.4 mm I.D. glass column packed with Gas Chrome Q solid support (100/120 mesh) which was coated (10 % loading) with Silar 10 C stationary phase. The gas chromatograph used was a Varian model 4600 equipped with a flame ionization detector. Nitrogen was used as the carrier gas at a flow rate of 30 ml/min. Flow rates of detector gases were 30 ml/min for hydrogen and 300 ml/min for air. Injector and detector temperatures were 225°C and column temperature was programmed to increase at a rate of 3°C/min from 150°C at the start of injection to 200°C. The detector was operated at the highest sensitivity setting. All fatty acids were eluted from the column within 45 minutes.

Fatty acids present in pike lipids were identified by comparison of peak retention times with those of known standards (MaxEpa oil), by reference to published studies on fatty acid composition of lipids from pike (Kluytmans and Zandee 1973; Kinsella et al. 1977) and other north-temperate freshwater fish (Ackman et al. 1967b; Hazel 1979a,b) and by combination capillary gas chromatography/mass spectrometry (done by Tony Wierzbick, courtesy of Dr. M.T. Clandinin). Detector response per unit weight of fatty acid was assumed to be the same for all fatty acids measured (Ackman and Sipos 1964; Albertyn et al. 1982). Concentrations of individual fatty acids in pike tissues were determined by comparing the area of individual chromatographic peaks with the area of the internal standard (13:0) peak. A sample containing known amounts of several fatty acids was routinely chromatographed to ensure that the accuracy of fatty acid quantification did not change (due to leaks in the system or sample adsorption) during the period of test sample analysis.

Chromatograms from liver and ovary NLs contained several peaks which were produced by unidentified compounds (probably furan fatty acids; Glass et al. 1974) and which overlapped with peaks of several PUFAs. Peaks from these unidentified compounds together represented about 10 % and 5

% of total peak area in chromatograms from liver and ovary NLs respectively. PUFAs were quantified independently of the unidentified compounds with the column argentation procedure of Glass et al. (1977) (which they devised for separating PUFAs from furan fatty acids) as follows. One portion of each sample of fatty acid methyl esters from NLs of liver and ovary was analyzed by gas chromatography as described previously and the quantity of each PUFA combined with that of co-eluting unidentified compounds determined. A second portion of each sample was dissolved in hexane, applied to a column of silica gel H containing 5 % w/w $AgNO_3$ (see Glass et al. 1977), and eluted with a 3:1 mixture of hexane/diethyl ether. All PUFAs remained on the column whereas saturated and monounsaturated fatty acids, the internal standard (13:0), and the unidentified compounds were quantitatively eluted. Gas chromatographic analysis of the eluate from the silica gel column revealed the quantity of each unidentified compound which was subtracted from the combined quantity of each PUFA plus co-eluting unidentified compounds (determined from G.C. analysis of the first sample portion) to give the quantity of each PUFA in the sample. The content of the unidentified compounds in the samples declined rapidly and unpredictably during storage (unlike the content of identified fatty acids) and therefore is not reported.

The NLFA content of ovary and liver was not measured in May 1987 because the $AgNO_3$ chromatography procedure was not working at that time. Ovary NLFA and PLFA content was not measured in August 1988 because seasonal changes in ovary fatty acid content had by this time been clearly described.

Calculations and Statistics

The carcass weight of pike was calculated as total body weight minus the sum of ovary and liver weight. The weight of organs and tissues and their fatty acid content is expressed relative to carcass weight. For each fish, the total content of NLFAs and PLFAs in an organ or tissue was calculated by multiplying NLFA and PLFA concentrations by relative organ or tissue weight. White muscle was assumed to have a relative weight of 550 g/kg carcass weight (Schwalme and Mackay 1985).

Levene's test (Snedecor and Cochran 1980) showed that sample variances were unequal ($p<0.05$) for 13 of the 23 variables studied. However, most variables with heterogenous variances exhibited large and well defined seasonal changes and therefore were not tested statistically for differences between sample means. One variable, muscle NLFA concentration, exhibited unequal sample variances and no clear seasonal variation. Therefore, the significance of seasonal variation in muscle NLFA concentration was tested using the Kruskall-Wallis non-parametric procedure ($p<0.05$). For variables with homogeneous sample variances, the overall null hypothesis (ie: all sample means are equal) was tested using one-way ANOVA ($p<0.05$). Multiple pairwise comparisons were done on variables with homogeneous sample variances and significant ANOVA results. The multiple comparison procedure used was the Ryan-Einot-Gabriel-Welsch multiple F (REGWF) test ($p < 0.05$) (SAS Institute Inc. 1988) because this procedure controls the maximum experimentwise error rate even if multiple comparisons are performed only after significant ANOVA results (see Bernhardson 1975).

Results

Organ and tissue weights

Pike in Lac Ste. Anne spawned in late April or early May. The weight of the recrudescing ovary began increasing in August 1987 and reached about 230 g/kg carcass wt by May 1988 (Fig. II-1a). Of the pike caught in May 1988, three had not spawned and still contained mature eggs and five had spawned all their eggs. The early part of ovarian recrudescence was accompanied by a doubling of liver weight from between 12 and 14 g/kg carcass wt in summer (May to August 1987) to 31 g/kg carcass wt by January, after which liver weight declined to summer values by June 1988 (Fig. II-1b). The weight of AP tissue did not show significant seasonal variation (Fig. II-1c).

Fatty Acid Concentrations

Concentrations of NLFAs and PLFAs in the ovary began increasing in August 1987 and by January reached levels of 1.15 and 2.83 % wet wt respectively which were maintained until March (Fig. II-2a,b). It is possible that ovaries of the unspawned pike caught in May 1988 were being resorbed and therefore had lower concentrations of fatty acids compared to ovaries of pike caught in January or March (Fig. II-2a,b). Throughout ovarian recrudescence PLFAs and NLFAs comprised, by weight, about 70 % and 30 % respectively of the sum of NLFA and PLFA concentrations in the ovary (Fig. II-2a,b).

Concentrations of NLFAs in the liver were high (7 % wet wt) in June, 1987, but thereafter declined steadily and remained at very low levels (0.5 % wet wt) between January and March before again reaching high levels (5 % wet wt) by June 1988 (Fig. II-2c). Concentrations of NLFAs in adipopancreatic tissue and muscle sometimes varied considerably between fish but did not show significant seasonal variation (Fig. II-2e,g).

All organs and tissues examined contained higher concentrations of PLFAs in fall and winter (September to March) than in summer (June to August) (Fig. II-2b,d,f,h). In liver and muscle, during the summer to winter period, increases in PLFA concentration were completed between July and September 1987, but in AP tissue and ovary the increase was protracted, lasting from July or August 1987 to January or March (Fig. II-2b,d,f,h). Maximum concentrations of PLFAs in winter exceeded minimum levels in summer by 4 fold in the ovary but by only 1.7, 1.5, and 1.3 fold in AP tissue, liver, and muscle respectively (Fig. II-2b,d,f,h).

Organ and tissue fatty acid content

The content of NLFAs and PLFAs in the ovary increased steadily between August 1987 and March 1988 (Fig. II-3 a,b).

Until January, accumulation of fatty acids in the ovary occurred by increases in both the concentration of fatty acids (Fig. II-2a,b) and increases in ovary weight (Fig. II-1a), but between January and March fatty acid accumulation occurred solely as a result of increases in ovary weight. Pike caught in March and unspawned pike caught in May 1988 contained similar amounts of NLFAs and PLFAs in their ovaries (Fig. II-3a,b) as a result of offsetting differences in ovary weight and fatty acid concentrations (Figs. II-1a, 2a,b).

Even though the liver doubled in weight between summer and winter (Fig. II-1b), its content of NLFAs declined from 1.1 g/kg carcass wt in June 1987 to 0.12 g/kg carcass wt in January before increasing to summer values by the following June (Fig. II-3c). The content of PLFAs in the liver increased from 0.14 g/kg carcass wt in June and July 1987 to 0.55 g/kg carcass wt in January and then declined to summer values by June 1988 (Fig. II-3d). A significant two fold increase in the PLFA content of adipopancreatic tissue occurred between July 1987 and March 1988, but the content of NLFAs in this tissue did not change seasonally (Fig. II-3e,f). Since the relative weight of white muscle (550 g/kg carcass wt) was assumed to remain constant throughout the year, changes in the estimated content of NLFAs and PLFAs in white muscle paralleled changes in their concentrations (Fig. II-2g,h). The implications of this assumption were considered in data interpretation.

Data in Fig. II-4 were obtained by summing the values in Figs. II-2g,h and II-3a to f, individually for each fish. Although they changed seasonally, quantities of NLFAs in ovary and liver (Fig. II-3a,c) were too small, relative to those in adipopancreatic tissue (Fig. II-3e) and muscle (Fig. II-2g), to produce significant seasonal changes in the total NLFA content of either the three somatic tissues combined (Fig. II-4a), or all four tissues combined (Fig. II-4b). In contrast, the total PLFA content of the somatic tissues (Fig. II-4c) and that of all tissues combined (Fig. II-4d) increased significantly during fall and winter and declined during spring. Between July 1987 and March 1988, the four tissues examined accumulated 5.4 g of PLFAs (per kg carcass wt) (Fig. II-4d) of which 4.6 g accumulated in the ovary (Fig. II-3b) and 0.8 g in the somatic tissues (Fig. II-4c). The seasonal accumulation of PLFAs in the somatic tissues was not enough to produce significant seasonal changes in the total fatty acid content of these tissues (Fig. II-4e).

From May to August the PLFA content of the four tissues examined (about 2 g/kg carcass wt; Fig. II-4d) amounted to about one-quarter of their content of NLFAs (7 to 9 g/kg carcass wt; Fig. II-4b). However, when the ovaries were nearing maturity in March their content of PLFAs together with that of the somatic tissues (7.3 g/kg carcass wt; Fig. II-4d) nearly equalled the combined NLFA content of the four tissues (8.5 g/kg carcass wt; Fig. II-4b). Consequently, the total content of fatty acids (NLFAs plus PLFAs) in the four tissues increased by about 60 % during ovarian recrudescence, from about 10 g/kg carcass wt in September to 16 g/kg carcass wt in March (Fig. II-4f). Comparison of Figs. II-4b,d, and f clearly shows that seasonal cycles in the total fatty acid content of the four major lipid depots of female pike are due to changes in the content of PLFAs; primarily the content of PLFAs in the ovary.

Discussion

Results in Fig. II-4 show that, from August to March, ovarian recrudescence in pike does not involve significant transfers of fatty acids from somatic to ovarian tissues or from NLs to PLs. Although tissue fatty acid contents in Fig. II-4 are expressed relative to carcass weight, they allow accurate assessment of fatty acid transfers from August to March because the carcass weight of female pike in Lac Ste. Anne changes by only 5 % during this period (Billard et al. 1983). If all fatty acids accumulated in the ovary and in the PL compartment of somatic and ovarian tissues between August 1987 and March 1988 originated solely through transfers of fatty acids from somatic to ovarian tissues and from NLs to PLs then the total fatty acid content of the somatic tissues and the combined NLFA content of all tissues should have declined by more than 50 % (Fig. II-4b,e). Such large declines clearly did not occur. Most of the fatty acids accumulated in the recrudescing ovaries and in the PLs of pike tissues before March probably originated from dietary nutrients pike consumed during ovarian recrudescence or possibly from body compartments such as skeletal bone (see Phleger et al. 1989) which were not examined.

Mobilization of fatty acids from somatic tissues may make a significant contribution to ovarian maturation between mid-March and spawning (late April/early May). According to Medford and Mackay (1978), the mature ovaries of a 900 g somatic weight pike contain about 8 g of lipid of which about 1.8 g becomes deposited after mid-March. Female pike in Lac Ste. Anne lose about 17 % of their somatic weight between March and May, probably from catabolism of muscle (Billard et al. 1983). In a 900 g somatic weight pike this amounts to a loss in muscle mass of about 153 g and a loss in somatic lipid content of about 1.5 g (assuming the lipid content of pike muscle to be 1 % of tissue wet wt). This approximately equals the amount of lipid deposited in pike ovaries after mid-March.

Seasonal changes in liver weight and liver NLFA and PLFA concentrations of pike may be associated with several factors including ovarian recrudescence and cycles in temperature and food intake. In teleosts, estrogens released from the recrudescing ovary initiate the synthesis of vitellogenin in the liver (Plack and Frazer 1971; Ng and Idler 1983) and enhance vitellogenin production by triggering both a large increase in liver weight (Ng and Idler 1983) and a marked proliferation of cellular organelles (endoplasmic reticulum, Golgi complex, and mitochondria) within liver cells (Ng et al. 1984; Mommsen and Walsh 1988). Therefore, increases in the weight and PLFA concentration of pike liver during ovarian recrudescence (Figs. II-1b and II-2d) probably reflect the liver's role in vitellogenin production. Increases in the PLFA concentration of liver during ovarian recrudescence may have resulted from both a proliferation of cellular organelles and an accumulation of vitellogenin awaiting its release from the liver.

The large depletion of NLFAs from pike liver during summer and fall of 1987 may also be related to the reproductive cycle because several studies have reported a nearly complete disappearance of cytoplasmic lipid droplets (which contain mainly NLs) from fish hepatocytes during vitellogenesis (Peute et al. 1978; van Bohemen et al. 1981; Ng and Idler 1983). In pike, NLFAs depleted from the liver during fall may have been catabolized for energy or incorporated into liver PLs or yolk precursors. Additionally, rapid accumulation of NLFAs in the liver during May and June 1988 may reflect the heavy feeding which pike indulge in after spawning (Diana 1979).

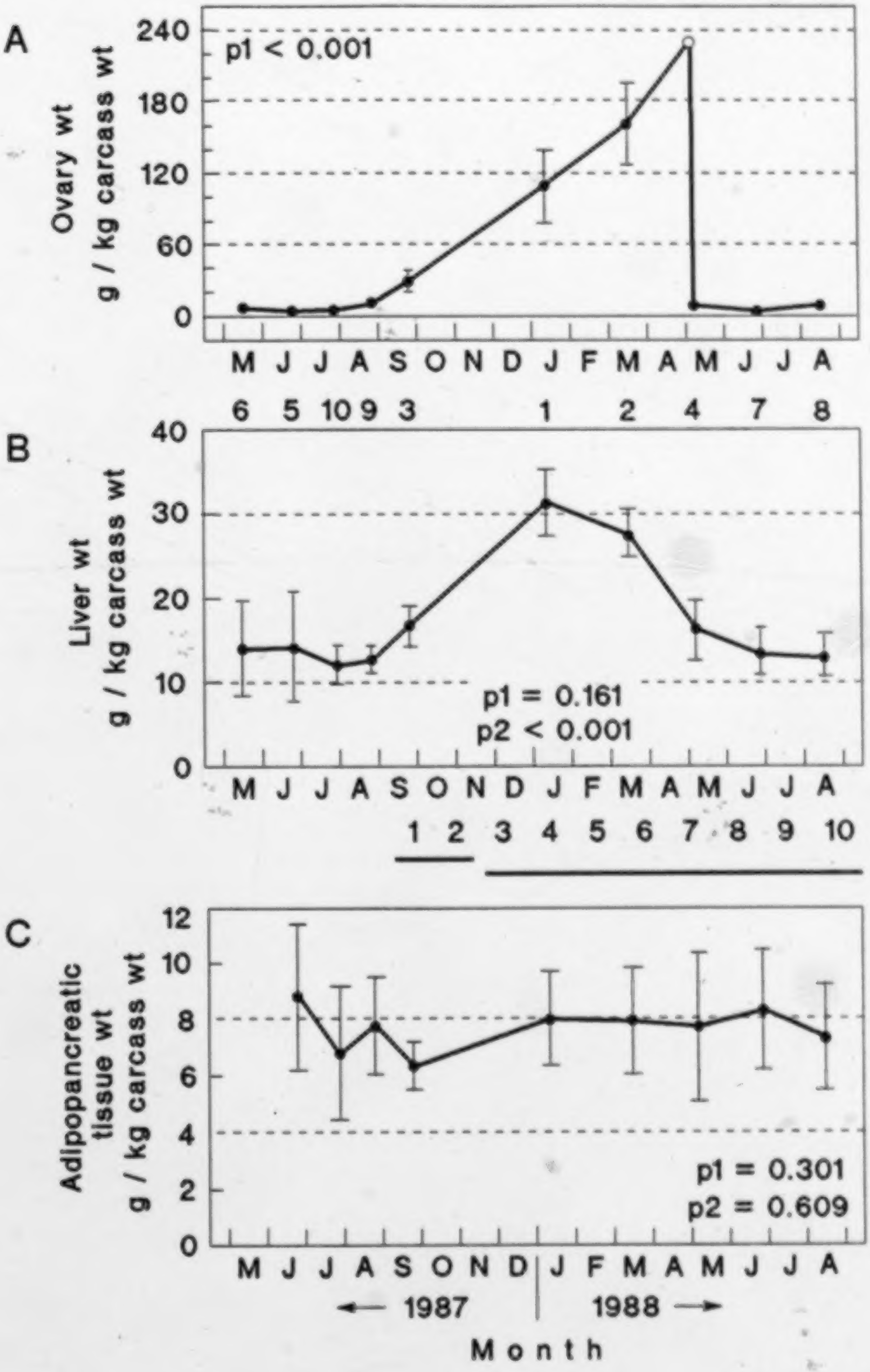
Seasonal changes in the PLFA concentration of pike muscle and adipopancreatic tissue are difficult to link directly to the reproductive cycle but may be related to temperature. The increase in PLFA concentrations of pike muscle and adipopancreatic tissue, and in part the increase in liver PLFA concentration, between August 1987 and January

1988 probably reflects the synthesis of new organelle membranes as an adaptation to low temperatures during winter. This proposal is supported by studies of Egginton and Sidell (1989) and Penny and Goldspink (1980) which suggest that the abundance of mitochondrial and sarcoplasmic reticulum membranes in fish muscle increases during cold acclimation. It is also worth noting that the increase in PLFA concentration in muscle (and liver) of pike began in August 1987 while water temperature was high and was completed by September, well before water temperatures in Lac Ste. Anne reached winter values (see Billard et al. 1983). This suggests that the environmental cue initiating increases in muscle PLFA concentration in nature may not be temperature (as in laboratory studies of cold acclimation) but some other factor, most likely photoperiod.

This study has shown that female pike undergo large seasonal cycles in ovary NLFA and PLFA content and smaller cycles in the PLFA content of their somatic tissues. Lack of seasonal changes in the NLFA content of muscle and AP tissue, the pike's major NL depots, can probably be attributed to the ability of pike to feed successfully year round (Diana 1979) and to their sedentary lifestyle which does not involve long migrational movements (Diana 1980). Perhaps for these reasons, pike do not need to accumulate large reserves of fatty acids in their somatic tissues in preparation for either migration, long periods of fasting, or for ovarian recrudescence.

Opposite page

Figure II-I. Seasonal changes in the weight (expressed per kg carcass wt) of ovary, liver, and adipopancreatic tissue of female pike. Shown are the means and 95 % confidence intervals (C.I.'s) of 5 to 8 fish per sample. C.I.'s are omitted if they are enclosed by the symbol. In May 1988, 3 pike were caught which had not spawned and still contained mature eggs (2 of these fish yielded accurate measurements of ovary weight) and 5 pike which had spawned all their eggs. Therefore, variables measured on, or including data from, ovaries have two means in May 1988 of which O shows the mean for the unspawned fish and ● shows the mean for the 5 spawned fish; data from the unspawned fish were not used in statistical tests on these variables. P values are shown for Levene's test of homogeneity of variances (p1) and for ANOVA (p2). When multiple comparisons were done on a variable (eg: panel B), sample means are numbered (from highest to lowest) on top of the panel and results of the Ryan-Einot-Gabriel-Welsch multiple F (REGWF) test are shown below the panel. Means underlined at the same level are not significantly different ($P < 0.05$).


A
p1 < 0.001
Ovary wt
g / kg carcass wt
0
60
120
180
240
M J J A S O N D J F M A M J J A
6 5 10 9 3 1 2 4 7 8
B
Liver wt
g / kg carcass wt
0
10
20
30
40
p1 = 0.161
p2 < 0.001
M J J A S O N D J F M A M J J A
1 2 3 4 5 6 7 8 9 10
C
Adipopancreatic
tissue wt
g / kg carcass wt
0
2
4
6
8
10
12
p1 = 0.301
p2 = 0.609
M J J A S O N D J F M A M J J A
← 1987
1988 →
Month

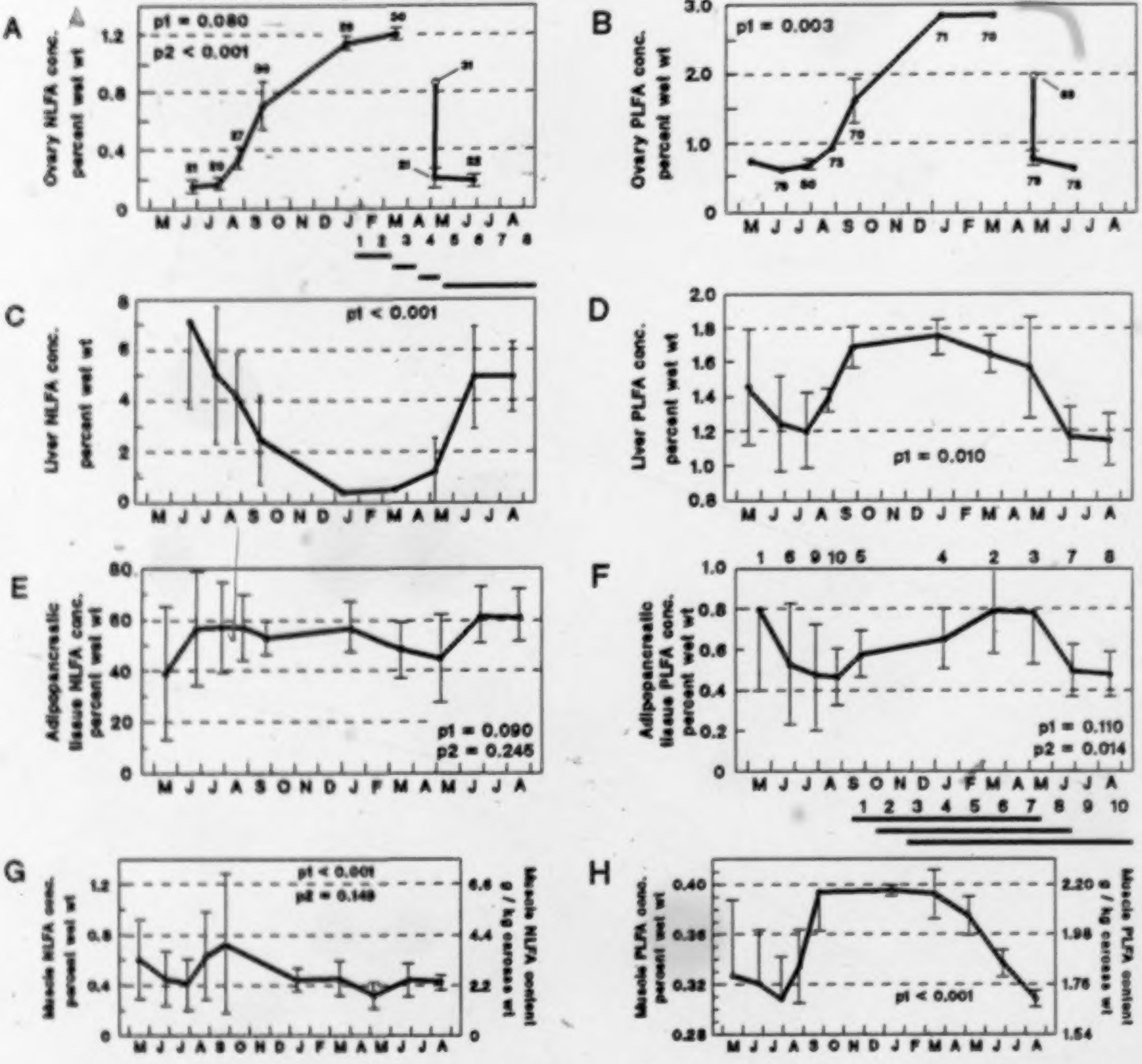


Figure II-2. Seasonal changes in the NLFA and PLFA concentrations of somatic and ovarian tissues and total NLFA and PLFA contents of white muscle in female pike. Numbers adjacent to the means in panels A and B are the concentrations of NLFA's and PLFA's expressed as a proportion of the sum of NLFA and PLFA concentrations. p1 shows the significance level for Levene's test of homogeneity of variance. p2 shows the significance level for the Kruskall-Wallis test in panel G and for ANOVA in panels A,E, and F. For some samples, half the C.I. is omitted for clarity. Other details as in Figure II-1.

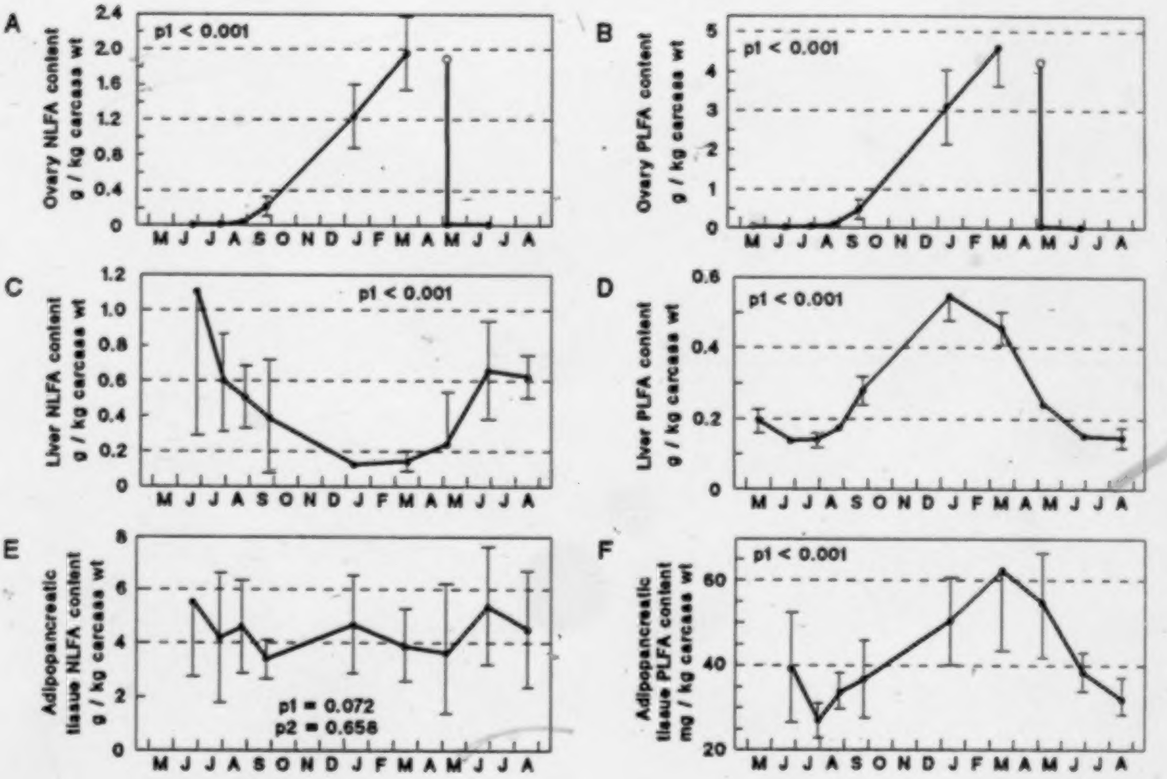


Figure II-3. Seasonal changes in the content of NLFA's and PLFA's in the ovary, liver, and adipopancreatic tissue of female pike. For some samples, half the C.I. is omitted for clarity. Details as in Figure II-1.

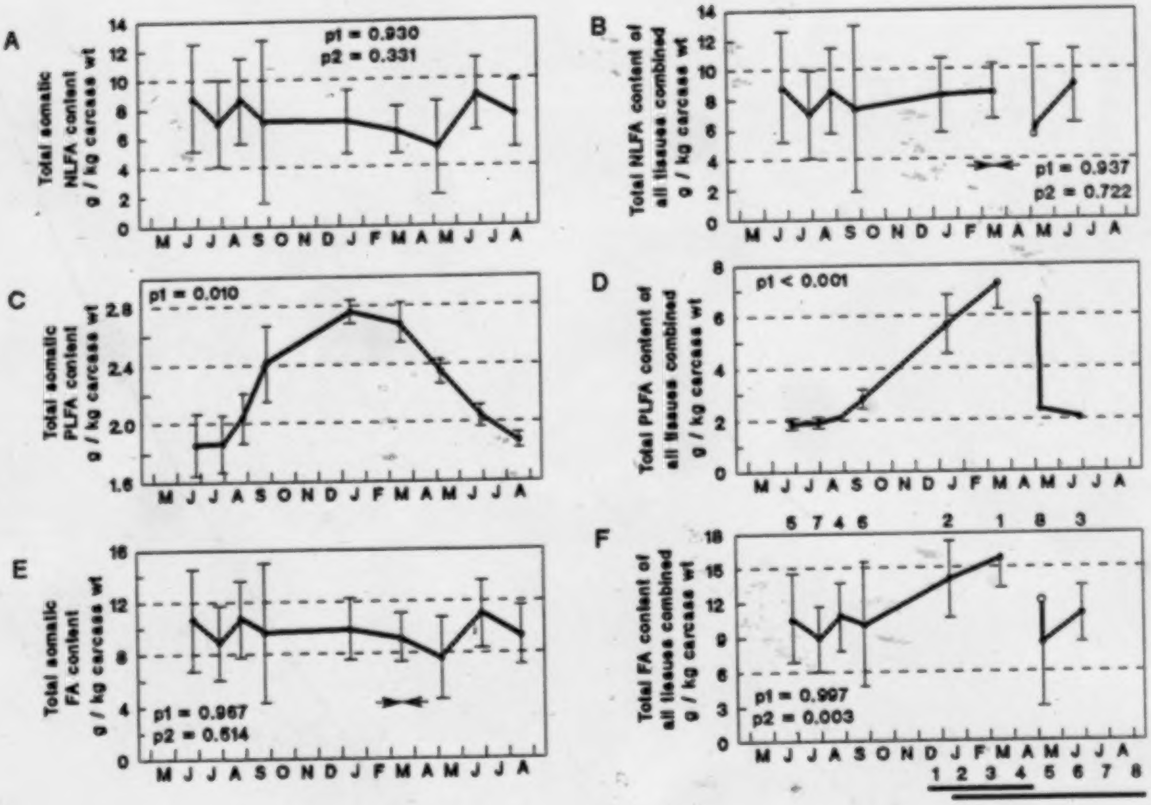


Figure II-4. Seasonal changes in the content of NLFA's, PLFA's, and total fatty acids (NLFA's and PLFA's combined) in the three somatic tissues combined and in all four tissues combined. In panel B the opposing arrows show the expected NLFA content of the somatic and ovarian tissues if all PLFA's accumulated in these tissues between August 1987 and March (5.1 g/kg carcass wt; Figure II-4d) had been derived from NLFA's. Opposing arrows in panel E show the expected total fatty acid content of the three somatic tissues if all ovarian fatty acids accumulated between August 1987 and March (6.4 g/kg carcass wt; Figures II-3a,b) had been derived from fatty acids in somatic tissues. For some samples, half the C.I. is omitted for clarity. Other details as in Figure II-1.

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Chapter III

Seasonal changes in the fatty acid composition of ovarian and somatic tissues of female northern pike (Esox lucius L.)

Introduction

In many north-temperate fish, seasonal cycles in reproduction, dietary intake, and temperature may create temporary imbalances between the dietary supply and physiological requirements for n-3 fatty acids. Particularly large imbalances may occur during winter when many fish require large amounts of n-3 fatty acids for ovarian maturation (Love 1980; Henderson and Tocher 1987) and temperature related membrane restructuring (Hazel 1989), yet experience great reductions in food intake (Diana 1979).

In fish, n-3 fatty acids, and to a lesser extent n-6 fatty acids, are regarded as essential dietary nutrients (Watanabe 1982; Stickney et al. 1983; Bell et al. 1986) and are required in large amounts during ovarian recrudescence because mature ovaries often comprise as much as 25 % of body weight and contain up to 10 % of wet weight as lipids (Kaitaranta and Ackman 1981; Henderson and Tocher 1987). Furthermore, ovarian lipids of many fish are predominantly polar lipids (PLs) which are typically much richer in polyunsaturated fatty acids (PUFAs) than neutral lipids (NLs) (Fogerty et al. 1986; Henderson and Tocher 1987). During winter there may also be requirements for increased incorporation of n-3 fatty acids into somatic PLs because the total content of polar lipid fatty acids (PLFAs) increases significantly during fall in several somatic tissues of fish (chapter II), and because cellular membranes become more unsaturated as part of the homeoviscous adaptation phenomenon (Hazel 1989).

The possibility of seasonal mismatches between the dietary intake and physiological requirements for n-3 fatty acids needs evaluation to determine whether commercial fish rations need to be altered to accommodate changes in essential fatty acid (EFA) requirements of fish in relation to seasonal and life history events. If imbalances between the intake and requirements for n-3 EFAs occur during winter one may expect north-temperate fish to preferentially divert dietary n-3 EFAs away from somatic NL reserves, or perhaps mobilize these fatty acids from NL reserves, so that n-3 EFAs can be conserved for ovary growth and seasonal membrane restructuring. Accordingly, the percentages of n-3 EFAs in somatic NLs would be expected to decline during fall and winter and perhaps be compensated for by increased percentages of monounsaturated fatty acids (MUFAs) to maintain the proper physical state (fluidity) of NL reserves (Hazel 1979b).

Although a few studies have examined seasonal changes in the fatty acid composition of fish, these studies possess limitations which make them unsuitable for evaluating the relationship between EFA intake and requirements. These limitations include the measurement of fatty acid composition on only total tissue lipids (Jangaard et al. 1967; Henderson et al. 1984; Bergstrom 1989), on few sampling dates (Roche and Peres 1984; Dutta et al. 1985; Agren et al. 1987), and in only one or two body compartments (Hardy and Mackie 1969; Eaton et al. 1975; Yuneva 1987; Henderson and Almatar 1989; Tidwell and Robinette 1990).

In the present study, seasonal changes in the fatty acid composition of NLs and PLs in the major lipids depots of female northern pike were measured to determine whether a reallocation of n-3 fatty acids from somatic NLs to ovarian lipids and somatic PLs occurs over winter. Pike were chosen for this study because they are abundant, widespread north-temperate fish which experience large seasonal cycles in temperature and food intake and grow their ovaries over winter.

Materials and Methods

This chapter reports seasonal changes in the fatty acid percent composition of the same pike for which fatty acid content is reported in chapter II. Accordingly, the methods of fish collection, tissue sampling, lipid extraction, and fatty acid analysis were those described in chapter II. One-way ANOVA ($p<0.01$) was used to determine the statistical significance of seasonal variation in the parameters measured.

Results

The objective of this study was to examine seasonal changes in the percentage and total content of individual fatty acids in the NLs and PLs of individual tissues and multi-tissue compartments (eg: somatic tissues) to determine whether EFAs are reallocated or transfered seasonally between body compartments. It was also useful to examine the fatty acid composition of tissue total lipids (TLs) to determine whether seasonal changes in the fatty acid composition of NLs or PLs were offset by opposite changes in the other lipid fraction within the same tissue. To a large extent, seasonal changes in the fatty acid composition of tissue TLs and the lipids of multi-tissue compartments reflected changes in the relative proportions of NLs and PLs and the relative weight of individual tissues. Therefore, differences in fatty acid composition between NLs and PLs and between different tissues will be described first before examining seasonal changes in the fatty acid composition of individual lipid fractions, tissues, and multi-tissue compartments.

The predominant fatty acids present in pike lipids were 14:0, 16:0, 18:0, 16:1n7, 18:1n9, 18:2n6, 20:4n6, 22:5n6, 18:3n3, 20:5n3, 22:5n3, and 22:6n3. Altogether, these fatty acids comprised 91 to 96 % of the total chromatogram peak area associated with non-furan acids.

Variation in fatty acid composition between NLs and PLs

Figs. III-1 to III-3 show the differences in fatty acid composition between NLs and PLs and between the individual tissues of pike. Because the extent of these differences was influenced by seasonal effects (described later), Figs. III-1 to III-3 show data for two dates, July 1987 and January 1988, at which the variables shown were at or near seasonal maximum or minimum values.

In all tissues, proportions of saturated fatty acids (SFAs) were higher in PLs (22 to 31 % of total fatty acid content) than in NLs (17 to 24 %). Monounsaturated fatty acids (MUFAs) were considerably more abundant in NLs (32 to 37 % in July, 36 to 50 % in January) than in PLs (13 to 25 %). In the somatic tissues, PLs always contained significantly higher percentages of polyunsaturated fatty acids (PUFAs) (43 to 57 %) than did NLs (35 to 40 %), but in the ovary this trend was only evident during recrudescence (Fig. III-1). Higher proportions of PUFAs in PLs than in NLs were due primarily to n-3 fatty acids because proportions of n-6 fatty acids differed little between the two lipid fractions (Fig. III-1).

There were large differences between individual fatty acids in their abundance in pike lipids. Of the SFAs, percentages of 16:0 were approximately twice those of 18:0 in both NLs and PLs (Figs. III-2,3). Proportions of 16:0 were always higher in PLs than NLs, whereas percentages of 18:0 were slightly higher in PLs than NLs in July, but not in January (Figs. III-2,3). The two MUFAs, 16:1n7 and 18:1n9, were much more abundant in NLs than PLs, and the percentage of 18:1n9 tended to exceed that of 16:1n7 in both NLs and PLs, especially in muscle PLs, liver NLs, and in the NLs of recrudescing ovaries (January) (Figs. III-2,3).

Docosahexaenoic acid (22:6n3) was the most abundant n-3 fatty acid in both NLs and PLs and occurred at much higher proportions in PLs (16 to 38 %) than in NLs (7 to 13 %) (Figs. III-2,3). In contrast, percentages of 18:3n3 were considerably lower in PLs (1.5 to 3 %) than in NLs (4 to 8 %). Polar lipids contained significantly higher proportions of 20:5n3 than NLs in January (Fig. III-3) but not in July (Fig. III-2). Proportions of 22:5n3 were low (1.5 to 2.5 %) and approximately the same in NLs and PLs (Figs. III-2,3). In all tissues, PLs contained lower proportions of 18:2n6 and higher proportions of 20:4n6 compared to NLs. Percentages of 22:5n6 were low (0.7 to 2.0 %) in both NLs and PLs but were slightly higher in the latter lipid fraction.

Variation in fatty acid composition between tissues

Fatty acid composition varied little between individual fish. Consequently, there were many significant differences in fatty acid composition between tissues, even though the magnitude of these differences was small for some fatty acids (Figs. III-1,2,3). In July, variation between tissues in the percentages of major fatty acid groups in NLs was limited to relatively small differences in the percentage of

SFAs and MUFAs. However, in January ovary and liver NLs contained substantially higher percentages of MUFAs and lower percentages of n-3 fatty acids compared to NLs of muscle and AP tissue. In July, percentages of the major fatty acid groups in PLs of ovary differed from those in liver, but by January the PLs of these organs were nearly identical in their percent composition of the major fatty acid groups (Fig. III-1). Differences in the percentages of MUFAs, PUFAs, n-3 and n-6 fatty acids between PLs of muscle and AP tissue were similar in direction and magnitude in January and July (Fig. III-1).

Among individual fatty acids the more prominent and consistent differences were lower percentages of 16:1n7 and 18:1n9 and higher percentages of 22:6n3 in PLs of muscle than in PLs of other tissues. The NLs of liver and recrudescing ovaries had higher percentages of 18:1n9, and muscle and AP tissue NLs had higher percentages of unidentified fatty acids than NLs of other tissues (Figs. III-2,3).

The fatty acid compositions of ovary and liver differed in July, but by January they became considerably more similar to each other and more distinct from the compositions of muscle and AP tissue. These changes are shown well by 16:0, 18:1n9, and 20:5n3 fatty acids in ovary and liver NLs and by 18:1n9, 22:6n3, and 20:4n6 fatty acids in PLs (Figs. III-2,3). Percentages of 22:6n3 in NLs were a notable exception to this trend; differences between ovary and liver were larger in January than in July (Figs. III-2,3).

In both July and January, muscle and adipopancreatic NLs had very similar fatty acid compositions (Figs. III-2,3). Although the fatty acid compositions of ovary and liver PLs became similar in January, for most fatty acids differences in % composition between the PLs of muscle and AP tissue were of similar direction and magnitude in January and July (Figs. III-2,3).

Seasonal changes in fatty acid composition of NLs and PLs

Major fatty acid groups

The percentage of SFAs on ovarian NLs declined from 23.6 % in July to 16.8 % in January 1987 and increased again the following spring. Clearly identifiable seasonal variations in the percentage of SFAs did not occur in the NLs of other tissues (Figs. III-4,5). Between late summer (August, September) and winter the NLs of all four tissues underwent significant increases in the percentage of MUFAs and decreases in PUFAs (Figs. III-4,5). These changes were of much larger magnitude in ovary and liver (8 to 16 wt %) than in muscle and AP tissue (4 to 5 wt %). From May to August 1988, MUFAs and PUFAs returned to the previous years levels in ovary and liver NLs but returned only partially in NLs of muscle and AP tissue. In NLs of ovary and liver, large seasonal changes (12 to 14 wt %) in the percentage of n-3 fatty acids were accompanied by smaller changes (4 wt %) in n-6 fatty acids, but in muscle and AP tissue NLs the n-3 fatty acids were the only polyunsaturates to change seasonally (Figs. III-4,5).

In all tissues, the percentage of SFAs in PLs decreased significantly from late summer to winter 1987 and increased fully to previous levels during the spring and summer of 1988 (Figs. III-6,7). Percentages of MUFAs in PLs increased during fall and winter and decreased during spring in liver and AP tissue and to a small extent in ovaries but did not change seasonally in muscle (Figs. III-6,7). In January, percentages of MUFAs temporarily became equal in PLs of liver and ovaries after being lower in liver PLs throughout most of the year. From June to March the percentage of n-3 fatty acids in ovarian PLs increased to a greater extent (9 wt %) than total PUFAs (5 wt %) as a result of concurrent decreases in the proportion of n-6 fatty acids (Fig. III-6). Of the four organs and tissues examined, only liver showed a significant decrease in the proportion of total PUFAs and n-3 fatty acids during fall and winter. As with the other major fatty acid groups, percentages of total PUFAs, n-3, and n-6 fatty acids in liver PLs became temporarily similar to those in ovary PLs during winter (Fig. III-6). Although statistically significant, seasonal changes in the proportions of n-6 fatty acids in liver PLs were small (about 1.5 wt %). Percentages of n-3 fatty acids in PLs of muscle and AP tissue increased significantly from June 1987 to March or May 1988 (Figs. III-6,7).

Individual fatty acids

In ovarian NLs, seasonal changes in wt % of total SFAs were due mainly to 16:0 which decreased from late summer to winter 1987 and returned fully to previous levels the following spring (Fig. III-8). Percentages of 18:0 in ovarian NLs decreased briefly in August 1987 but by January they returned close to levels prevailing during early summer (Fig. III-8). Percentages of 16:0 in liver NLs were higher in spring (June 1987, May 1988) than at other times of year (Fig. III-9). In contrast, 18:0 in liver NLs was present in highest percentages from September to March and this partially offset seasonal changes in 16:0 so that the wt % of total SFAs in liver NLs did not show significant seasonal change (Figs. III-4,9). Muscle NLs did not show significant seasonal changes in the percentage of 16:0 or 18:0 (Fig. III-10). Although percentages of these fatty acids in NLs of AP tissue changed significantly (Fig. III-11), the peaking of 16:0 in June 1987 was not repeated in 1988 and the magnitude of changes in 18:0 was quite small (0.6 wt %).

Percentages of 16:1n7 and 18:1n9 increased greatly between late summer and winter of 1987 in NLs of ovary but, of the two MUFAs, only 16:1n7 changed significantly in NLs of liver, muscle and AP tissue (Figs. III-8 to 11). During the spring and summer of 1988 percentages of 18:1n9 returned close to previous levels in ovary NLs and 16:1n7 returned to previous levels in liver NLs but only partially returned in NLs of other tissues (Figs. III-8 to 11).

In the NLs of all four tissues the dominant seasonal change among the n-3 fatty acids was a large significant decline in the percentage of 22:6n3 between late summer and winter of 1987, followed by an increase in the spring of 1988 (Figs. III-8 to 11). Percentages of 20:5n3 also showed substantial declines from late summer to winter in NLs of ovary and liver and 22:5n3 showed smaller but significant declines during this period in NLs of all four tissues (Figs. III-8 to III-11).

Ovary and liver NLs underwent significant declines in the percentage of 20:4n6 from September to January with a return to previous levels the following spring (Figs. III-8,9). Percentages of 22:5n6 showed small but significant declines during fall and winter in NLs of ovary (Figs. III-8). Ovary NLs exhibited seasonal increases in the proportion of 18:2n6 between August and January 1987 whereas in liver NLs 18:2n6 increased throughout summer (June to August in both 1987 and 1988) but decreased between August and January 1987 (Figs. III-8,9). None of the three n-6 fatty acids underwent substantial seasonal changes in weight percentage in NLs of muscle or AP tissue (Figs. III-10,11).

Seasonal changes in the fatty acid composition of PLs included declines in percentages of 16:0 and 18:0 from summer to winter and increases during spring in all four tissues (Figs. III-12 to III-15). Seasonal declines in the percentage of 18:0 in PLs began earliest in ovary (June 1987; Fig. III-12) and latest in AP tissue (September 1987;

Fig. III-15). Changes in the percentage of 18:0 in muscle PLs were considerably smaller (about 1 wt %) than in PLs of other tissues (2.5 to 5.5 wt %)(Figs. III-12 to III-15).

Considerable variation existed between tissues in the type of seasonal changes exhibited by individual MUFAs in PLs. In liver PLs both 16:1n7 and 18:1n9 showed clearly defined increases during fall and winter and decreases during spring whereas in PLs of ovary and AP tissue only 16:1n7 underwent such changes (Figs. III-12,13,15). Percentages of 18:1n9 in ovary PLs (and possibly in AP tissue PLs) appeared to undergo two cycles per year; decreasing from June to September 1987, then increasing until January before declining again until May, and finally increasing again as a result of spawning in May 1988 (Fig. III-12). Neither 16:1n7 nor 18:1n9 changed substantially in muscle PLs (Fig. III-14).

Among the four tissues, ovary and liver displayed the largest seasonal changes in n-3 and n-6 fatty acid composition of PLs and, as in NLs, the percentage of 22:6n3 varied more than that of any other polyunsaturated fatty acid (Figs. III-12,13). In ovary PLs the wt % of 22:6n3 increased rapidly from June to September, then increased more slowly until May before decreasing again as a result of spawning (Fig. III-12). However, in liver PLs the proportion of 22:6n3 decreased between May and June in both years, remained relatively constant between June and September 1987, then decreased until January before increasing again until May 1988 (Fig. III-13).

Percentages of 18:3n3 and 20:5n3 also underwent small but significant seasonal changes in PLs of ovary, liver, and AP tissue. In all these tissues, the proportion of 18:3n3 in PLs increased from summer to winter but the timing of changes in 20:5n3 was specific to each tissue (Figs. III-12,13,15). The n-6 fatty acid composition of PLs underwent large seasonal changes only in ovarian tissues where the proportion of 20:4n6 decreased by 7 wt % from May to January 1987 (Fig. III-12). Small increases (0.5 to 1 wt %) in the percentage of 18:2n6 during late summer or winter also occurred in PLs of ovary and liver (Figs. III-12,13). None of the n-3 or n-6 fatty acids exhibited large seasonal changes in muscle PLs (Fig. III-14).

Seasonal changes in the fatty acid composition of TLs

Seasonal changes in the fatty acid composition of total lipids (TLs) reflected not only the composition of NLs and PLs but also the ratio of NL to PL (chapter II) because the two lipid fractions differed in fatty acid composition. In ovarian TLs the percentage of SFAs and n-6 fatty acids decreased from July to January 1987 (Fig. III-16) due to decreases in the percentage of these fatty acids in both NLs and PLs (Fig. III-4). Increases in the percentage of MUFAs in ovary TLs during fall and winter (7 wt %; Fig. III-16) were smaller than those in NLs (20 wt %; Fig. III-4) because PLs comprised 70 % of TLs in the ovaries and had relatively stable percentages of MUFAs (Fig. III-6). The percentage of

PUFAs in ovary TLs increased briefly from July to September 1987 but then declined to previous levels by January as a result of decreases in the PUFA percentage in NLs (Fig. III-4). Decreases in the percentage of n-3 fatty acids in ovary NLs from August to January (Fig. III-4) only partially offset the increases of these fatty acids in PLs (Fig. III-6) so that the percentage of n-3 fatty acids in ovary TLs underwent a significant increase (7 wt %) in late summer of 1987 which was maintained until the following spring (Fig. III-16).

During fall and winter, liver TLs exhibited increases in the percentage of SFAs, and n-3 fatty acids and decreases in the percentage of MUFAs and n-6 fatty acids (Fig. III-16). Except for the n-6 fatty acids, changes in the fatty acid composition of liver TLs were largely the reverse of those that occurred in the NLs and PLs (compare with Figs. III-4,6). These changes in liver TLs reflected the large increase, during fall and winter, in the content of PLFAs (Fig. II-3) which contained higher percentages of SFAs, PUFAs, and n-3 fatty acids and lower percentages of MUFAs compared to NLs (Fig. III-1). The only seasonal change in the fatty acid composition of muscle TLs was a small (3 wt %) decrease in the percentage of SFAs during fall and winter (Fig. III-17). In AP tissue, seasonal changes in the fatty acid composition of TLs (Fig. III-17) were very similar to those in NLs (Fig. III-5) because PLs comprised only a very small (about 1.5 wt %) portion of TLs in this tissue (Fig.

II-3).

Fatty acids whose percent composition showed relatively large (> 2.5 wt %) changes in ovary TLs from summer to winter were 16:0, 18:0, and 20:4n6 which decreased during this period and 16:1n7 and 18:1n9 which increased (Table III-1). Percentages of 22:6n3 in ovary TLs increased from about 15 % in June 1987 to 21 % in September and then remained relatively stable until May (Table III-1). In liver TLs, the largest seasonal changes were increases in the percentage of 16:0 and 22:6n3 and decreases in 18:1n9, 18:2n6, and 18:3n3 from summer to winter (Table III-1). Notable seasonal changes in muscle TLs were limited to declines in the percentage of 16:0 and increases in 16:1n7 from June or July 1987 to March 1988. In AP tissue, seasonal changes in the proportion of individual fatty acids in TLs were similar to those in NLs (compare Table III-1 and Appendix 1).

Seasonal changes in the fatty acid composition of combined lipids of somatic and ovarian tissues

Major fatty acid groups

The combined NLs of the three somatic tissues exhibited increases in the percentage of MUFAs and decreases in total PUFAs and n-3 fatty acids from summer to winter (Fig. III-18) as a result of similar changes in each individual tissue (Figs. III-4,5). Percentages of SFAs in somatic NLs declined from June to August 1987 and thereafter remained relatively constant and the n-6 fatty acids increased slightly during summer and declined during fall and winter (Fig. III-18). The inclusion of ovarian NLs with somatic NLs increased the magnitude of these changes, especially the changes in MUFAs (compare Figs. III-18,19).

As all three somatic tissues exhibited declines in the percentage of SFAs in PLs during fall and winter, and increases during spring (Figs. III-6,7), similar changes also occurred in the combined PLs of these tissues (Fig. III-18). The proportion of MUFAs in somatic PLs increased during winter (Fig. III-18), mainly as a result of similar changes in liver PLs (Fig. III-6). Increases in the percentage of total PUFAs in somatic PLs from June 1987 to May 1988 resulted from small increases of these fatty acids in muscle PLs (Fig. III-7) and from increases in the content of PLFAs in muscle (Fig. II-2) which contained higher percentages of polyunsaturates than PLs of either liver or AP tissue (Fig. III-1).

The inclusion of ovarian PLs with somatic PLs considerably altered the pattern of seasonal change in fatty acid composition (Fig. III-19). In combined PLs of somatic and ovarian tissues the summer to winter increases in MUFAs were considerably larger (7 wt %) than in somatic PLs alone (3 wt %) and the percentages of total PUFAs and n-3 fatty acids declined significantly during early winter unlike in somatic PLs (Fig. III-19). These changes reflected the higher percentages of MUFAs and lower percentages of PUFAs in ovarian PLs compared to PLs of somatic tissues (Fig. III-

1).

In somatic TLs (Fig. III-18) and somatic plus ovarian TLs (Fig. III-19) the percentages of SFAs and MUFAs differed significantly between the ten collection dates, but clear seasonal trends were not evident. Percentages of n-3 PUFAs in somatic TLs increased until September 1987 and steadily decreased throught the winter until the following May (Fig. III-18).

From May to September 1987 and in June 1988, ovaries contained very little lipid compared to other tissues and so the fatty acid composition of combined TLs of somatic plus ovarian tissues was identical to that of somatic TLs alone (compare Figs. III-18 and III-19 and Tables III-6 and III-7). In January and March ovaries contained more lipid but, nevertheless, percentages of MUFAs, PUFAs, n-3 and n-6 fatty acids in somatic plus ovarian TLs still resembled those in somatic TLs alone. This was a result of the close similarity in fatty acid composition between TLs of mature ovaries and that of the combined TLs of the three somatic tissues (compare Figs. III-16 and III-18 and Tables III-1 and 6).

Individual fatty acids

Although the percentages of many fatty acids changed seasonally in the NLs, PLs, and TLs of somatic tissues and combined somatic and ovarian tissues (Tables III-2 to 7), large (> 2.5 wt %) changes occurred in only four fatty acids - 16:0, 16:1n7, 18:1n9, and 22:6n3. Proportions of 16:0 decreased by 3.1 to 3.6 wt % from June 1987 to March 1988 in somatic NLs (Table III-2) and combined NLs of somatic plus ovarian tissues (Table III-4) and decreased by about 3.0 % from summer to winter in somatic PLs (Table III-3). Increases of 3.2 to 5.2 wt % in 16:1n7 from summer 1987 to winter 1988 occurred in NLs and TLs of somatic tissues (Tables III-2,6) and in the NLs and PLs of somatic plus ovarian tissues (Tables III-4,5).

Percentages of 18:1n9 in NLs and TLs of somatic tissues and somatic plus ovarian tissues (Tables III-2,4,6,7) decreased by 2.8 to 4.6 wt % from June to August or September 1987 and increased from September to May or June of 1988. In the combined PLs of somatic plus ovarian tissues (Table III-5) the percentage of 18:1n9 increased by 2.9 wt % from July 1987 to January 1988 and returned to summer values during the following spring. Docosahexaenoic acid (22:6n3) underwent large seasonal changes of 4.3 to 5.6 wt % in NLs of somatic tissues (Table III-2) and in NLs, PLs, and TLs of somatic plus ovarian tissues (Tables III-4,5,7) and the timing of these changes generally paralleled changes in the total n-3 fatty acids of these lipid fractions (compare with Figs. III-18,19).

Mass balance evaluation of seasonal fatty acid transfers

Pike generally exhibited much larger variation, seasonally and between fish, in the total NLFA and PLFA content of their tissues than in fatty acid percent composition. Consequently, seasonal changes in the content (g/kg carcass wt) of individual and major groups of fatty acids in the NLs and PLs of pike tissues closely paralleled changes in total NLFA and PLFA content (chapter II), rather than changes in percent composition. Table III-8 shows the total content of major fatty acid groups in important body compartments of pike so that the possibility of selective seasonal transfers of certain types of fatty acids between body compartments can be evaluated. There were no significant ($p<0.01$) seasonal changes in the content of any fatty acid group in either the combined NLs or TLs of the somatic tissues or in the combined NLs of ovarian plus somatic tissues (Table II-8). Therefore, there does not appear to have been large seasonal transfers of any major fatty acid group from somatic to ovarian tissues or from NLs to PLs of female pike.

Discussion

This study provides evidence that female pike need to conserve limited dietary supplies of n-3 PUFAs during winter if they are to meet their physiological requirements for these essential nutrients. Specifically, the significant decreases in the percentage of n-3 PUFAs which occur during early winter in the NLs of somatic tissues (Figs. III-4,5,18) suggest that pike may either mobilize these fatty acids from, or divert dietary n-3 PUFAs away from, somatic NLs. The n-3 PUFAs conserved in this way would be available for use in ovarian construction and membrane restructuring. Additionally, decreases in the percentage of n-3 PUFAs in NLs of maturing pike ovaries (Fig. III-4) may be an adaptation to conserve these EFAs for storage in oocyte polar lipids and later use as components of cellular membranes in the developing embryo. This adaptation has been proposed by Weigand and Idler (1985) in regard to ovarian development in atlantic salmon.

Admittedly, the quantity of n-3 PUFAs conserved through reduction in the percentage of these fatty acids in somatic NLs makes only a modest contribution to the accumulation of n-3 PUFAs in ovarian TLs and somatic PLs over winter. From August 1987 to March 1988, 1.98 g of n-3 PUFAs accumulate in the recrudescing ovaries and an additional 0.28 g accumulate in somatic PLs (Table III-8). The 3.9 weight % decline in the percentage of n-3 PUFAs in somatic NLs from August 1987 to March 1988 (Table III-2) conserves about 0.31 g of n-3 PUFAs (0.039 X 8 g of fatty acids in somatic NLs - Fig. II-4). This represents only 14 % of the 2.26 g of n-3 PUFAs which accumulate in ovarian TLs and somatic PLs from August to March.

Although decreases in the percentage of n-3 PUFAs in somatic NLs conserve only modest amounts of these EFAs, the physiological limitations imposed on pike by reductions in dietary intake of n-3 PUFAs over winter may be substantial. One should remember that pike possess very small reserves of NLs compared to most fish (see Henderson and Tocher 1987) and sole reliance on somatic NLs to supply all the fatty acids needed for ovarian recrudescence would severely deplete these reserves of n-3 PUFAs and other fatty acids

(Table III-8). A 3.9 wt % decline in the percentage of n-3 PUFAs in somatic NLs may be all the pike can spare without jeopardizing the quantity of its NL energy reserves or altering their physical state (ie: fluidity). Furthermore, even modest reductions of dietary EFAs over winter can have serious non-lethal consequences by contributing to reduced growth or a delay in ovarian recrudescence so that fish are unable to spawn every year. In fact, populations of pike and other fish species in the arctic appear to grow mature ovaries only every second or third year, apparently because they are unable to obtain a sufficient quantity or quality of nutrients (Miller and Kennedy 1948; Kennedy 1953,1954; Roussow 1957; Geen et al. 1966). Shortages of dietary EFAs during winter may also be more severe in species that do not feed during winter or are transplanted outside their native range into environments that are possibly sub-optimal (Cunjak et al. 1987; Cunjak 1988).

Prior to March, there are no large transfers of any fatty acid class from somatic to ovarian tissues or from NLs to PLs. Quantities of individual fatty acid classes accumulated in the ovaries by March are greater than 50 % of the content of the same class in somatic TLs at the start of ovarian recrudescence in August (Table III-8). Therefore, if any fatty acid class accumulated in the ovaries solely as a result of transfer from somatic tissues then the content of that class in somatic TLs should have declined significantly (ie: by more than 50 %). Such large transfers did not occur because there were no significant seasonal changes in the content of any fatty acid class in somatic TLs (Table III-8). Similarly, lack of significant seasonal change in the content of any fatty acid class in the combined NLs of somatic and ovarian tissues (Table III-8) indicates there were no large transfers of fatty acids from NLs to PLs.

It is difficult to accurately quantify small transfers of fatty acids between body compartments because of the large variation between fish in the fatty acid content of tissue NLs. From August 1987 to March 1988 the content of n-3 PUFAs in somatic NLs appeared to decrease by about 0.82 g (Table III-8) which is more than sufficient to account for the 0.31 g of n-3 PUFAs represented by declines in the percentages of these fatty acids in somatic NLs. However, changes in the n-3 PUFA content of somatic NLs were not statistically significant (Table III-8). Therefore, it is not known whether seasonal changes in the percentage of n-3 PUFAs in somatic NL reserves result primarily from mobilization of these fatty acids from the reserves or simply from diversion of dietary n-3 PUFAs away from somatic NLs.

Although pike do not transfer large amounts of fatty acids from somatic to ovarian tissues, comparison of fatty acid content between pike and other fish helps considerably to identify physiological and environmental factors which favour such transfers. A good example of a fish which relies entirely on somatic tissues to provide nutrients to the maturing ovaries is the altantic herring. Atlantic herring accumulate much greater quantities of NLs in their somatic tissues (from 13 to 25 % of wet wt) than pike (1.0 to 1.7 % wet wt; Table III-2) and do not feed during ovarian recrudescence (Henderson and Almatar 1989). The mature eggs of atlantic herring possess total lipid contents (6 to 7 % of wet wt) and proportions of PLs and NLs (74 % PLs and 26 % NLs) similar to those of pike eggs (Henderson and Almatar 1989; Medford and Mackay 1979; Fig. II-2a,b). However, in herring the percentage of PUFAs in egg TLs (44 %) is more than double that in somatic NLs (18 %), whereas in pike the percentage of PUFAs in egg TLs (42 %) and somatic NLs (34 to 39 %) are more equal. The low percentage of PUFAs in herring NLs appears to reflect their diet of calanoid copepods which are rich in MUFAs but poor in PUFAs (14 to 23 % of total fatty acids) (Sargent et al. 1989). Because the percentage of PUFAs is much higher in herring eggs than in the rest of the body, PUFAs must be preferentially transferred from somatic to ovarian lipids during ovarian recrudescence. Thus, a comparison between pike and atlantic herring confirms expectations that selective transfers of fatty acids between somatic and ovarian tissues will be greater in fish that do not feed during ovarian recrudescence, accumulate large amounts of NLs in somatic tissues, and display marked differences in fatty acid composition between ovarian and somatic lipids.

Among the four organs and tissues examined, the largest seasonal changes in fatty acid composition, in both NLs and PLs occurred in the ovaries and liver (Figs. III-4 to III-15). This undoubtedly reflects the large changes which ovaries and liver undergo in their organ weight, lipid content, and cellular and tissue ultrastructure in association with the annual reproductive cycle (Ng et al. 1984; Mance 1987). In early summer the lipid content of ovaries is very low and its fatty acid composition is mainly that of connective tissue. But as the ovaries begin to accumulate nutrients in late summer their fatty acid composition reflects primarily that of egg nutrients such as lipovitellin and oil globules.

The fatty acid composition of fish eggs varies greatly between different species (Kaitaranta and Ackman 1981; Tocher and Sargent 1984), but few explanations for the adaptive significance of this variation have been offered. It is generally believed that fish species with longer developmental periods between hatching and first feeding produce eggs with greater NL content and which therefore have higher proportions of SFAs and lower percentages of PUFAs compared to eggs of species with faster larval development (Mommsen and Walsh 1988). Lipids of eggs (and of other tissues) of marine species have higher ratios of n-3 to n-6 fatty acids than lipids of freshwater species and this is thought to reflect differences in diet fatty acid composition (Ackman 1967).

Data presented in this chapter provide additional insight into the adaptive significance of fatty acid composition in fish eggs. Comparison of Figs. III-16 and III-18 and Tables III-1 and III-6 shows that ovarian and somatic TLs resemble each other in the percent composition of the major fatty acid classes much more closely when the ovaries are nearing maturity in January and March than in June and July. This suggests that very young pike fry have a similar fatty acid composition to that of adults. Since fry and adult pike inhabit the same general environment they may have similar fatty acid requirements and thus similar fatty acid compositions.

Changes in the fatty acid composition of NLs in maturing pike ovaries resemble the pattern which occurs in atlantic salmon (Weigand and Idler 1985) and may therefore represent a widespread phenomenon. As oocyte maturation proceeds, ovarian NLs of both pike and atlantic salmon exhibit highly significant increases in the percentages of 16:1n7 and 18:1n9 and decreases in 20:5n3 and 22:6n3 (Fig. III-8; Weigand and Idler 1985). The latter authors hypothesized that these changes represent an adaptation to make MUFAs available as sources of energy for the embryo and to spare n-3 PUFAs for storage in oocyte polar lipids. Additional support for this hypothesis is provided by observations that salmon embryos preferentially catabolize 16:1n7 and 18:1n9 for energy and preferentially retain 22:6n3 as part of membrane polar lipids (Hayes et al. 1973)

Seasonal changes in the fatty acid composition of pike liver appear to be related to the annual cycle of ovarian recrudescence. Such a relationship is indicated by the high degree of similarity between liver and ovary in the fatty acid composition of TLs and PLs in January and March (Figs. III-6,16 and Table III-1). Furthermore, fish liver is known to incorporate large amounts of lipid into vitellogenin, the main precursor of oocyte yolk, in response to ovarian estrogen hormones (Mommsen and Walsh 1988).

Because the fatty acid composition of vitellogenin presumably resembles that of the maturing oocyte, seasonal changes in the fatty acid composition of pike liver PLs may be due to the accumulation of vitellogenin in the liver. However, several considerations suggest that this is not the primary cause of seasonal changes in the fatty acid composition of liver PLs. First, even if increases in the PLFA concentration of liver from July 1987 to January (from 1.2 to 1.75 % of wet wt; Fig. II-2) were due entirely to vitellogenin accumulation, vitellogenin would represent no more than about 31 % of total liver PLFA content. This would not be enough to make the fatty acid compositions of ovary and liver PLs as similar as they are in January and March (Fig. III-6). Furthermore, estrogen induced proliferation of organelles likely contributes greatly to the observed increases in the concentration and total content of PLFAs in liver during winter (Ng et al. 1984; Mommsen and Walsh 1988). Finally, previous studies have shown that vitellogenin occurs only at very low concentrations in vitellogenic fish livers, apparently because it is secreted into the bloodstream shortly after being synthesized (van Bohemen et al. 1982). Therefore, it is likely that the bulk fatty acid composition of liver membrane lipids comes to resemble that of ovarian PLs during early winter (September to January) the period of peak vitellogenesis. This is reasonable because similar fatty acid compositions of vitellogenin and liver membrane lipids ought to simplify regulation of lipid synthesis within the endoplasmic reticulum of liver cells.

If changes in the PL fatty acid composition and fatty acid metabolism which occur in pike liver during fall and winter are primarily associated with vitellogenesis then much of the voluminous work on homeoviscous adaptation in fish liver may need to be re-evaluated. Changes in PL fatty acid composition (Hazel 1979a), and the rates of fatty acid and lipid synthesis (Hazel and Prosser 1979; Hazel 1990), fatty acid elongation and desaturation (Sellner and Hazel 1982; Hagar and Hazel 1985), and incorporation of specific fatty acids into lipids (Holub et al. 1977; Hazel 1983), observed in fish liver in response to temperature acclimation in the laboratory may be entirely different from what occurs seasonally in wild fish.

Caution must be exercised when attempting to ascribe seasonal changes in the degree of unsaturation of tissue PLs of pike (Figs. III-6,7) to the homeoviscous adaptation phenomenon. Changes in the ratio of saturated to unsaturated fatty acids in bulk PLs may simply reflect changes in the relative abundance of different membrane types and different PL classes rather than to alterations in the degree of unsaturation in individual membranes. Furthermore, changes in fatty acid composition of a membrane do not always indicate that viscosity changes as well. Nonetheless, in several studies, temperature related changes in the fatty acid compositions of bulk tissue PLs qualitatively resembled the changes seen in the predominant membrane types (Cossins 1976; Hazel 1979a; Bly et al. 1986). This suggests that decreases in the percentage of SFAs which occurred during fall and winter in the PLs of all three somatic tissues examined (Figs. III-6,7) were at least partly associated with the seasonal temperature cycle.

Declines in the percentage of SFAs during late summer and early winter were the most consistent seasonal changes observed in the fatty acid composition of tissue PLs; changes in the magnitude of MUFAs and PUFAs were highly variable between tissues (Figs. III-6,7). This is significant because the greatest effect on membrane physical state results from the addition of a single double bond to a saturated hydrocarbon chain (Coolbear et al. 1983). The percentage of SFAs relative to that of unsaturated fatty acids is therefore considered to be the primary determinant of membrane viscosity and not the relative percentages of MUFAs versus PUFAs (Cossins et al. 1978; Hazel 1989).

Although seasonal changes in the percentage of SFAs in pike PLs appear to be related to temperature, it is likely that other factors are involved as well. In muscle PLs of pike, the percentage of SFAs began to decline in June 1987, long before water temperature declined, and in 1988 it continued to increase after summer temperatures had been attained in June (Fig. III-7). Lack of close correlation between water temperature and the degree of unsaturation of PLs was also observed in the Black Sea anchovy (Yuneva et al. 1987). In anchovy, the percentage of SFAs in muscle PLs was minimal from January to July and thus spanned considerable portions of both the cold and warm seasons (Yuneva et al. 1987).

In previous studies, cold acclimation did not significantly alter the viscosity or the percentage of SFAs in sarcoplasmic reticulum membranes of goldfish white muscle (Cossins et al. 1978), nor did it decrease the percentage of SFAs in bulk PLs of mitochondrial membranes from carp red muscle (Wodtke 1981). Thus, my findings of significant seasonal changes in the percentage of SFAs (primarily 16:0) in pike white muscle PLs somewhat contrast with the published literature and suggest that it may be worthwhile to continue looking for environmentally induced changes in the membrane composition of white muscle in non-cyprinid fish species.

Seasonal changes in the fatty acid composition of pike NL depots support Hazel's (1979b) suggestion that the degree of unsaturation of fish NL reserves may influence the physical state (viscosity) of these reserves and the rapidity with which they can be hydrolysed to supply energy. In all four tissues of pike, declines in the percentage of PUFAs in NLs during fall and winter are offset specifically by increases in MUFAs (Figs. III-4,5). If the fatty acid composition of NLs had no effect on the physical state or physiological functioning of these lipids, one would not expect such close temporal correlation between reciprocal seasonal changes in the percentage of PUFAs and MUFAs (Figs. III-4,5). Therefore, increases in the percentage of MUFAs in pike NLs during fall and winter may be an adaptation to compensate for reductions in PUFAs and thereby maintain proper NL viscosity. Seasonal changes in the percentage of MUFAs in pike NLs are due mainly to 16 and 18 carbon MUFAs which appear to be ideally suited to increase lipid fluidity during winter because they are more mobile than longer chain fatty acids (Quinn 1981).

Reciprocal changes in the percentages of short chain versus long chain fatty acids appear to be prominent features of seasonal fatty acid cycles in northern pike and in other fish. In pike, increases in the percentages of 18:2n6 or 18:3n3 or both of these fatty acids occurred during early winter in the NLs of ovary, liver, white muscle, and AP tissue, and in liver PLs, while percentages of long chain n-3 and n-6 PUFAs either remained constant or more commonly declined (Figs. III-8,9,10,11,13). From June to August, muscle NLs of Black Sea anchovy exhibit reciprocal changes in 14:0 versus 16:0, 16:1n7 versus 18:1n9, and 20:5n3 versus 22:6n3; percentages of the short chain fatty acids increase while those of longer chain fatty acids decrease (Yuneva et al. 1987).

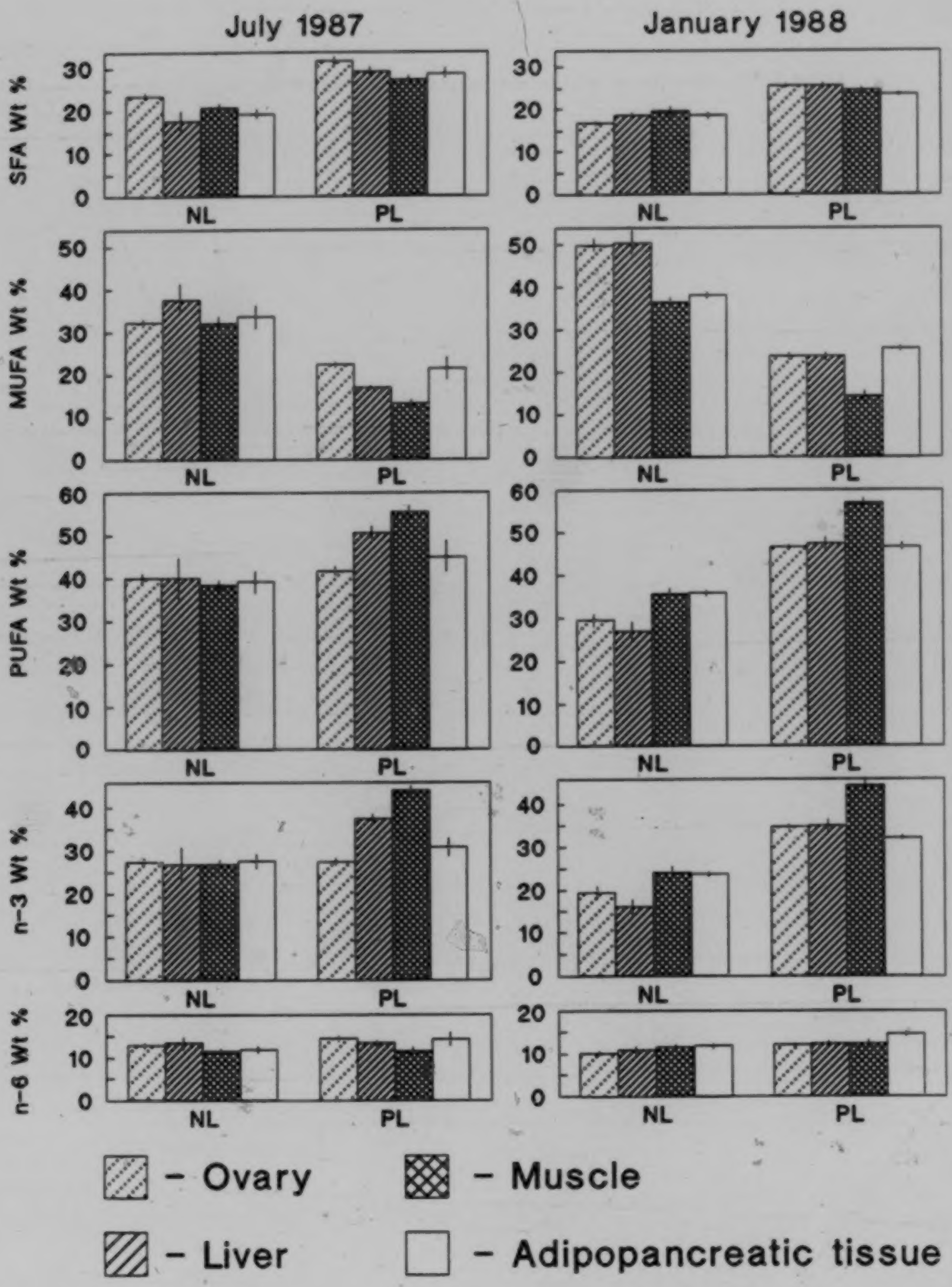
Reciprocal changes in the fatty acids of Black Sea anchovy appear to be due to the preferential transfer of long chain fatty acids from muscle NLs to the recrudescing ovaries (Yuneva et al. 1987). In pike, reciprocal changes in 18:2n6 and 18:3n3 versus long chain PUFAs in somatic tissues may be due to preferential diversion of long chain PUFAs to ovarian tissues or perhaps to changes in the activity of elongase and desaturase enzymes. Declining food intake during early winter may reduce circulating insulin levels which in turn reduce the activity of elongase and delta-6 and delta-5 desaturase enzymes (Jeffcoat 1979; Brenner 1981) so that 18 carbon PUFAs accumulate while longer chain PUFAs decrease in abundance.

In summary, female northern pike exhibit marked seasonal changes in the fatty acid composition of somatic and ovarian tissues which appear to be related to several environmental and physiological factors. Decreases in the percentage of n-3 PUFAs in somatic NLs during winter may reflect attempts to conserve limited dietary supplies of these fatty acids for use in ovarian construction and membrane lipid restructuring. Seasonal changes in the fatty acid composition of liver NLs and PLs appear to reflect the liver's role in vitellogenesis. Changes in the percentage of

SFAs in tissue PLs may be at least partly attributable to seasonal temperature cycles. Data presented in this study can serve as a useful reference for experimental studies designed to more clearly delineate the influence of ovarian, recrudescence, diet, and temperature on the fatty acid composition of wild fish.

Opposite page

Figure III-1. Comparison of fatty acid composition (major fatty acid groups) between tissues and between neutral lipids (NL) and polar lipids (PL) of pike. Quantities of fatty acids (ie: wt %) are expressed as a percentage of the total weight of fatty acids in tissue NL or PL. Means and 95 % confidence intervals (C.I.'s) are shown. Sample size for all variables is 6 in July 1987, and in January 1988 sample size is 6 for data on muscle and 7 for data on all other tissues.


July 1987
January 1988
SFA Wt %
MUFA Wt %
PUFA Wt %
n-3 Wt %
n-6 Wt %
0
10
20
30
40
50
60
NL
PL
Ovary
Muscle
Liver
Adipopancreatic tissue

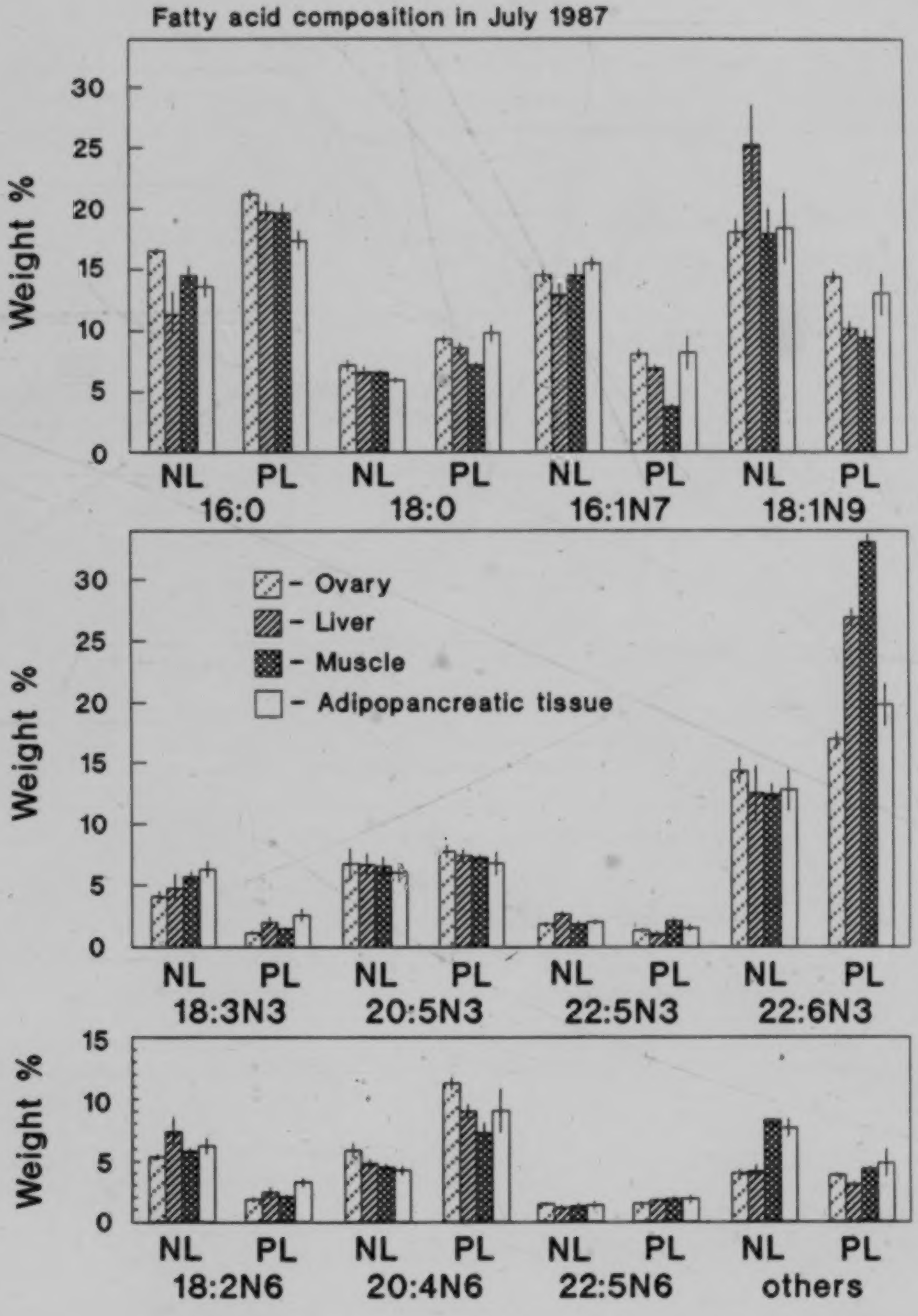


Figure III-2. Comparison of fatty acid composition (individual fatty acids) between tissues and between neutral lipids (NL) and polar lipids (PL) of pike in July 1987. Other details as in Figure III-1.

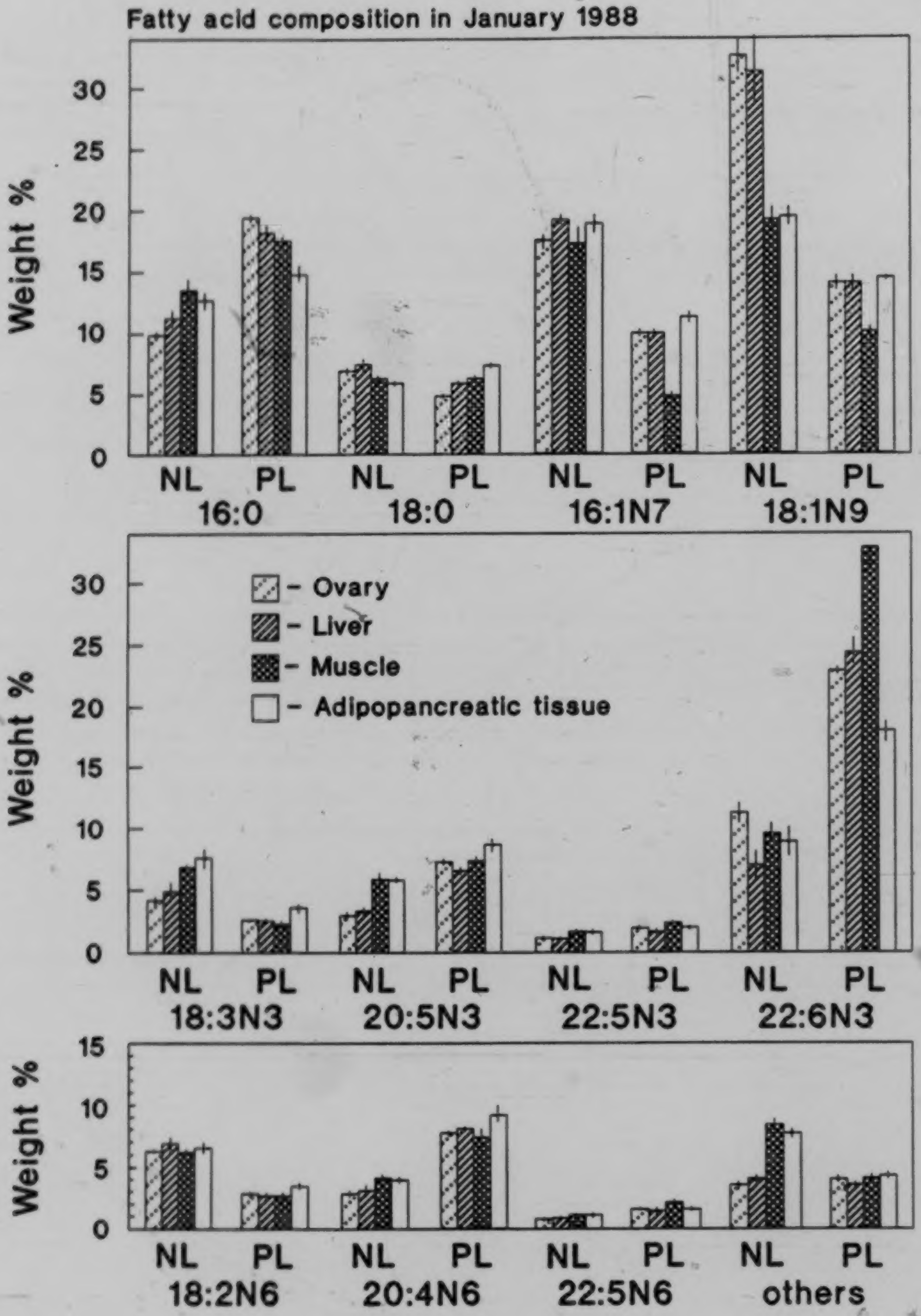
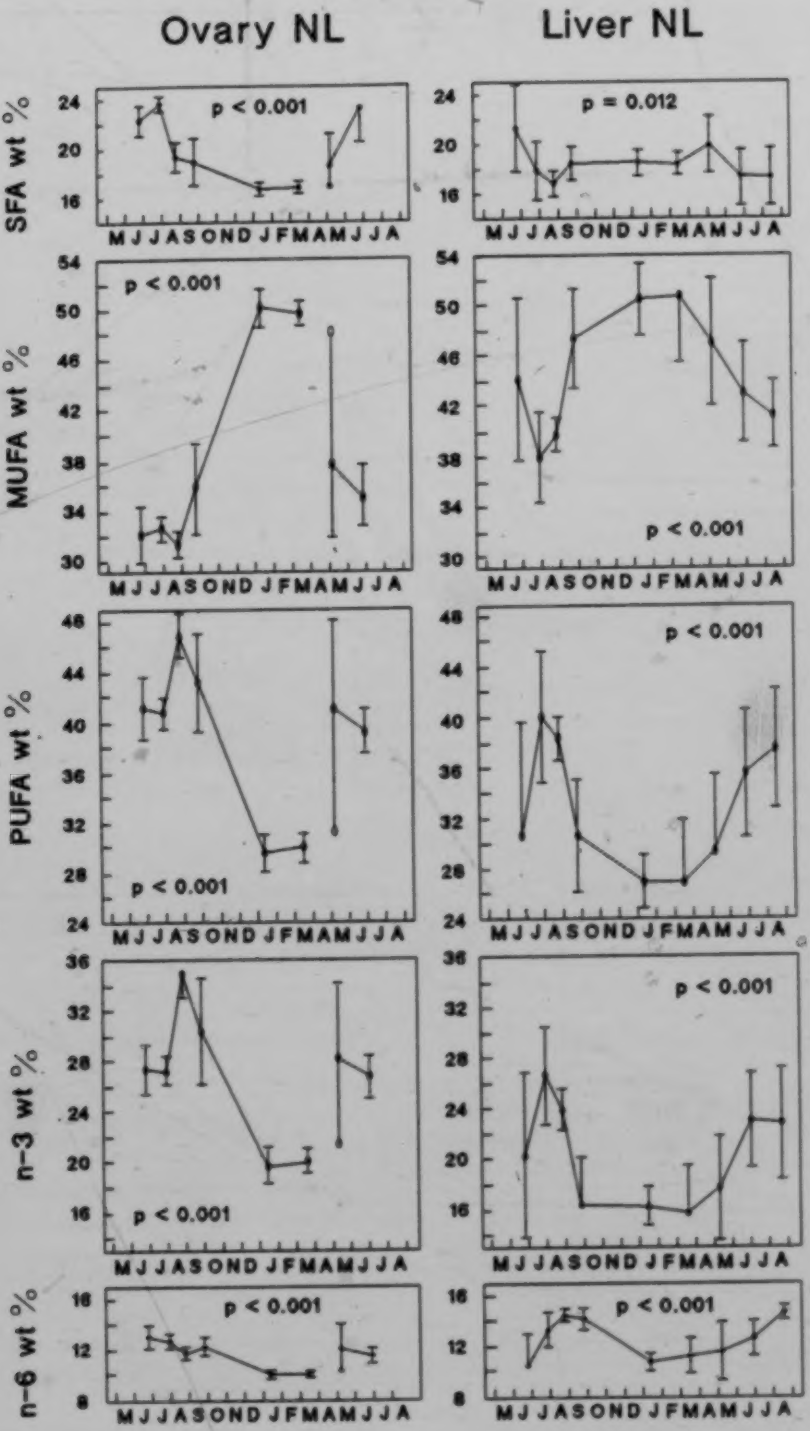


Figure III-3. Comparison of fatty acid composition (individual fatty acids) between tissues and between neutral lipids (NL) and polar lipids (PL) of pike in January 1988. Other details as in Figure III-1.

Opposite page

Figure III-4. Seasonal changes in the percentage of major fatty acid groups in the neutral lipids (NL) of ovary and liver of pike. Shown are the means and 95 % C.I.'s of 5 to 8 pike per sample. Exact n values for Figures III-4 to III-15 are given in Appendices 1 and 2. For some samples, half the C.I. is omitted for clarity. C.I.'s are omitted entirely if they are enclosed by the symbol. In May 1988, variables measured on, or including data from, ovaries have two means of which O shows the means for 3 pike which had not spawned and still contained mature eggs and ● shows the means for 4 pike which had spawned. Data from the unspawned fish were not used in statistical tests and are shown without C.I.'s. P values show the significance of seasonal variation for each variable as tested using one-way ANOVA.


Ovary NL
Liver NL
SFA wt %
MUFA wt %
PUFA wt %
n-3 wt %
n-6 wt %
p < 0.001
p = 0.012
p < 0.001
p < 0.001
p < 0.001
p < 0.001
p < 0.001
p < 0.001
p < 0.001
p < 0.001
M J J A S O N D J F M A M J J A
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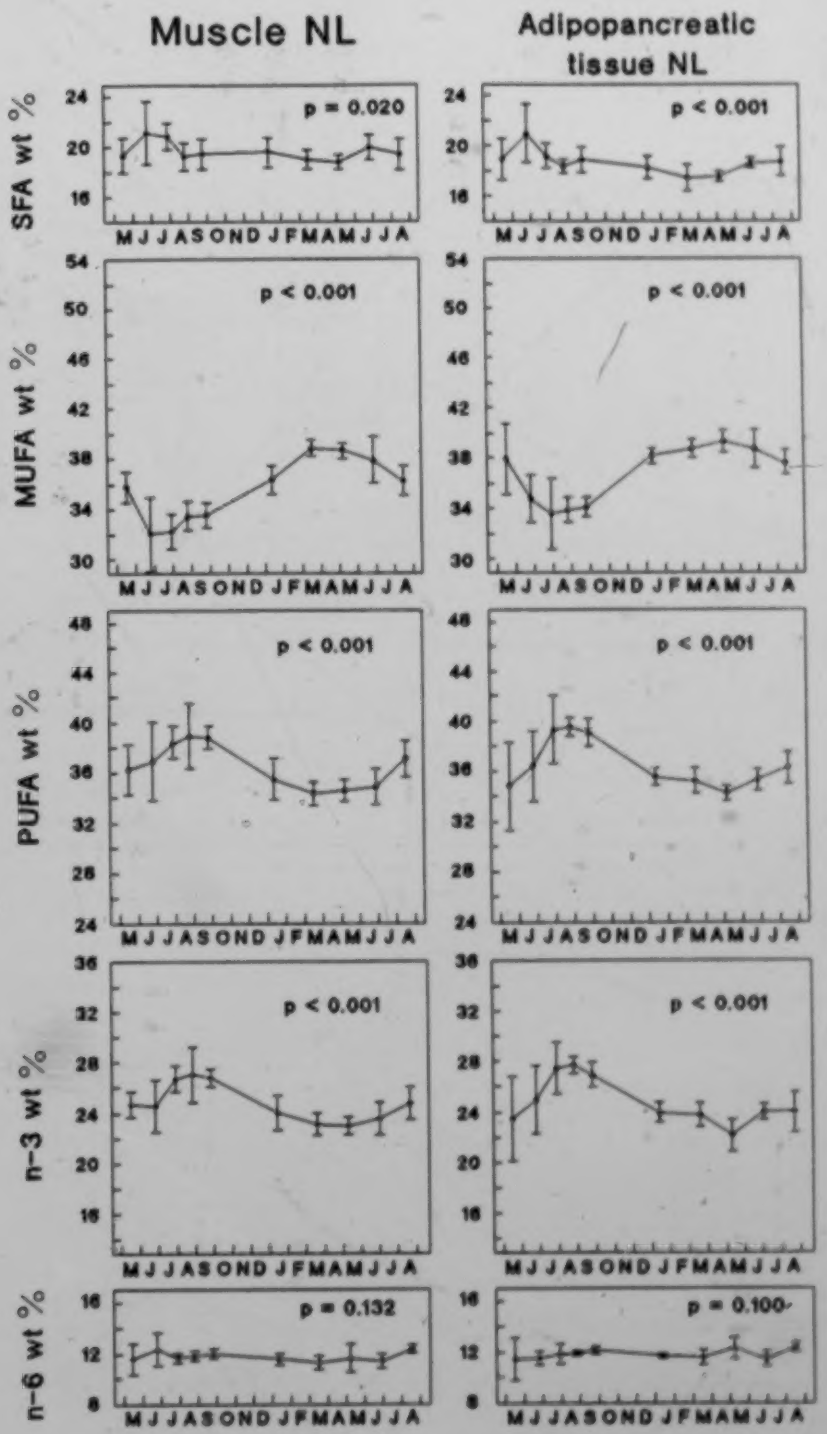


Figure III-5. Seasonal changes in the percentages of major fatty acid groups in neutral lipids (NL) of white muscle and adipopancreatic tissue of pike. Other details as in Figure III-4.

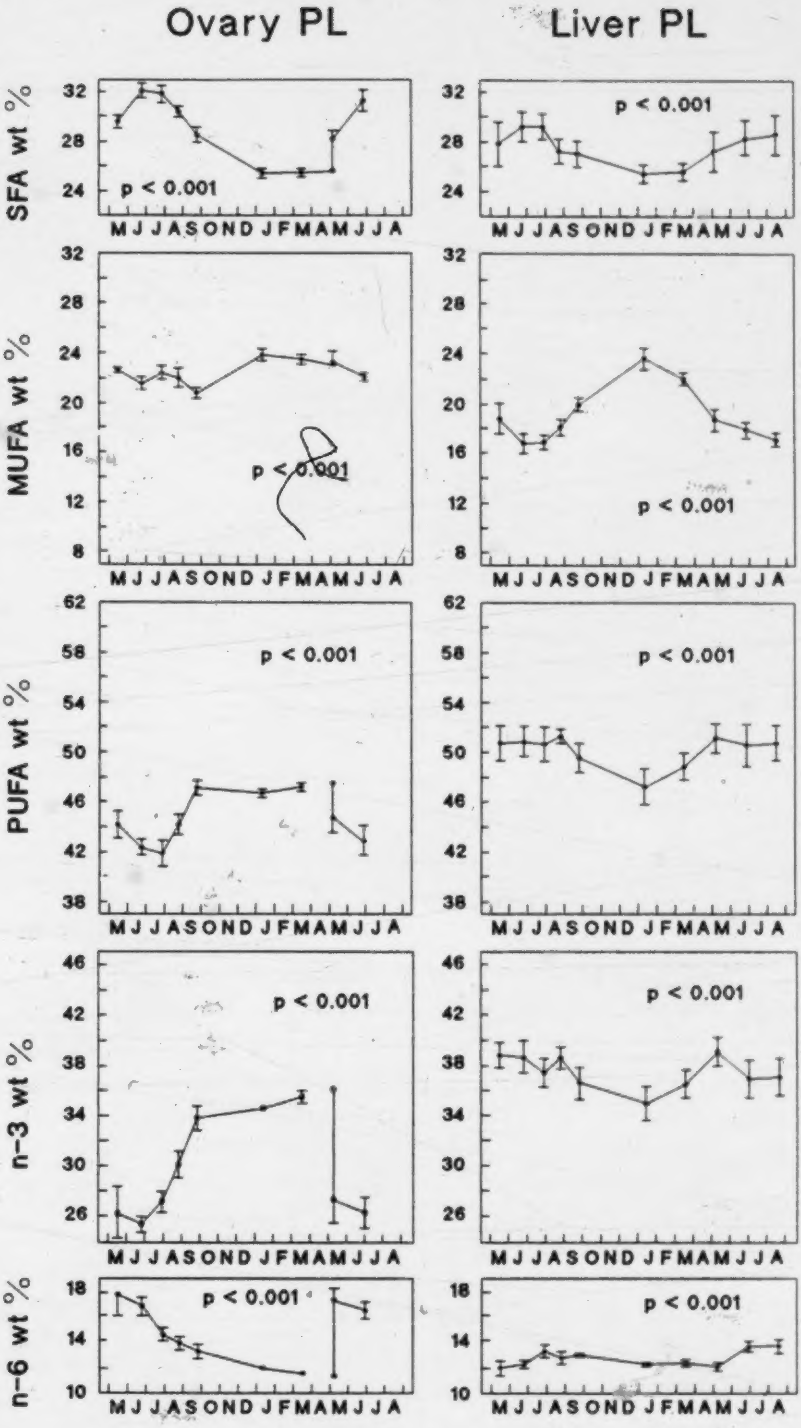


Figure III–6. Seasonal changes in the percentages of major fatty acid groups in polar lipids (PL) of ovary and liver of pike. Other details as in Figure III–4.

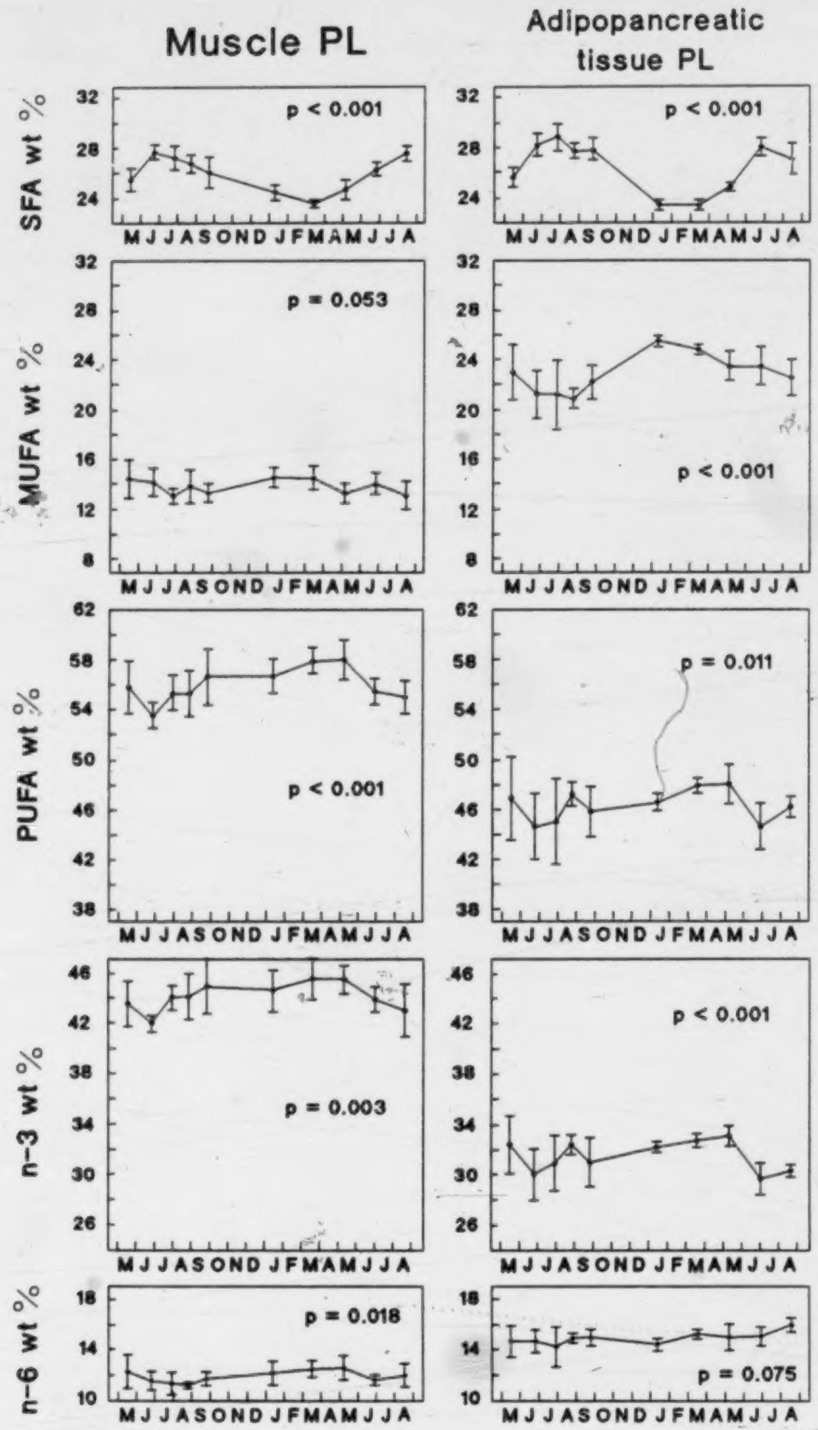


Figure III-7. Seasonal changes in the percentages of major fatty acid groups in polar lipids (PL) of white muscle and adipopancreatic tissue of pike.
Other details as in Figure III-4.

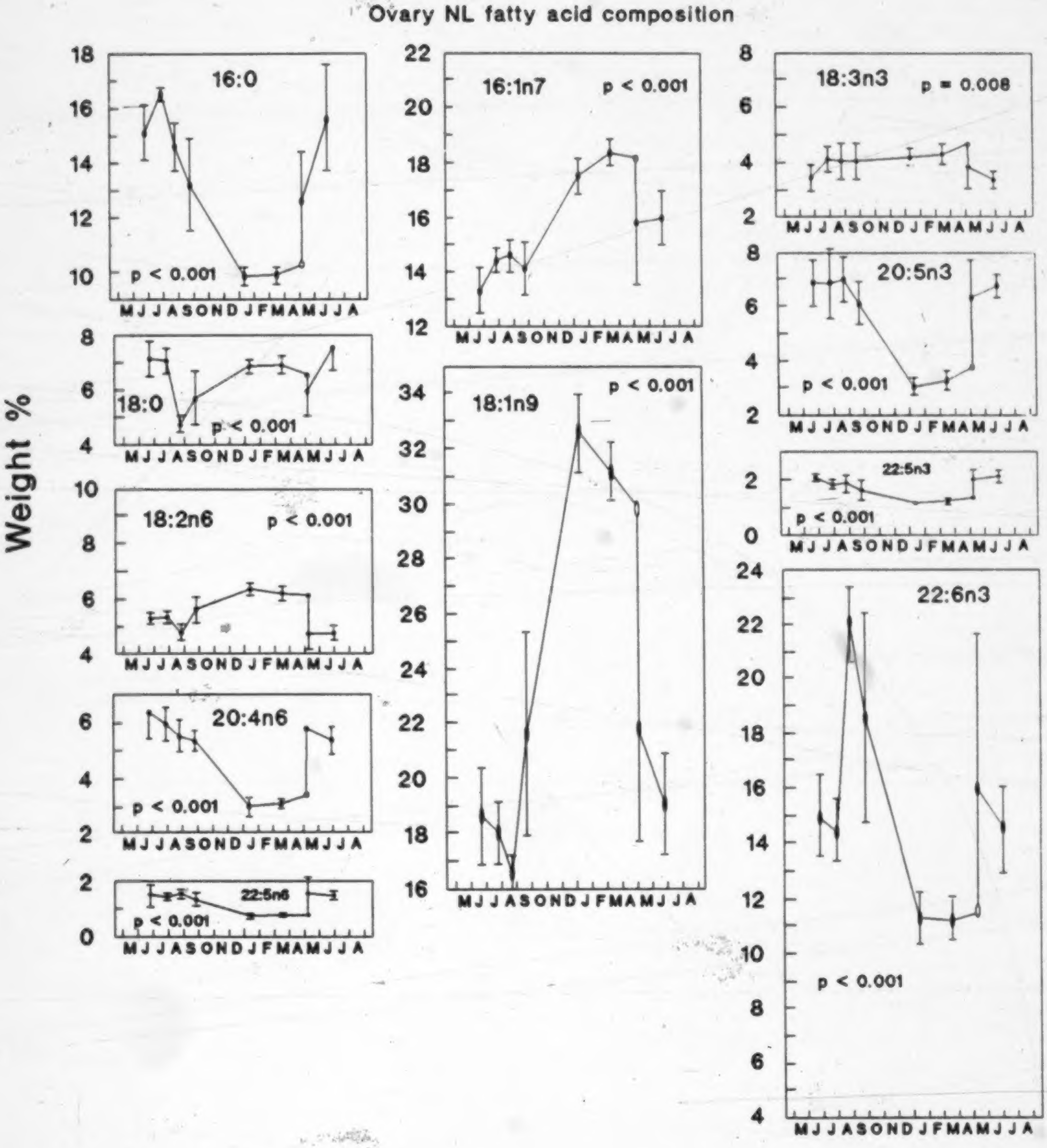


Figure III-8. Seasonal changes in the percentage of individual fatty acids in neutral lipids of ovaries of pike. Other details as in Figure III-4.

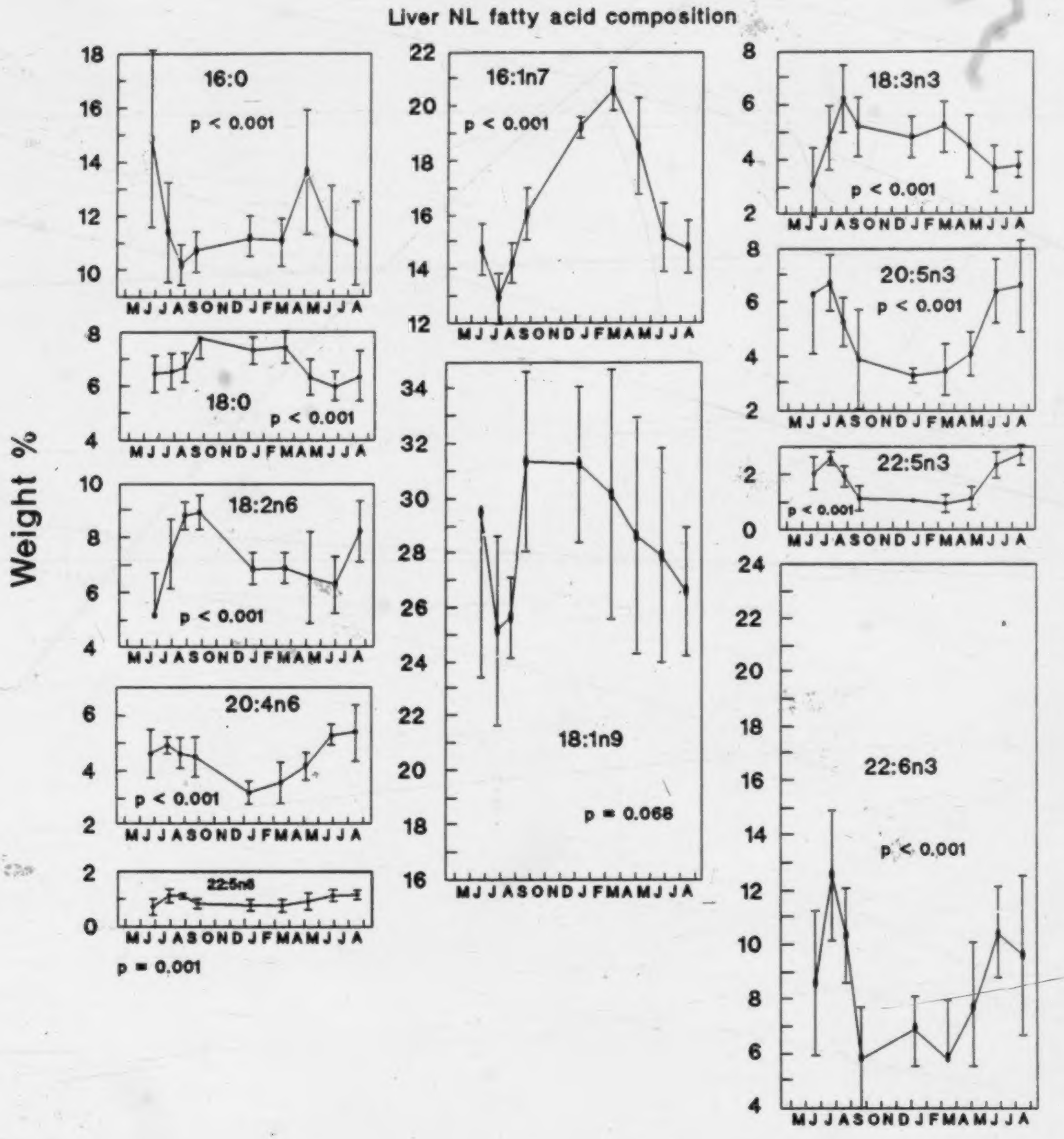


Figure III-9. Seasonal changes in the percentages of individual fatty acids in neutral lipids of liver of pike. Other details as in Figure III-4.

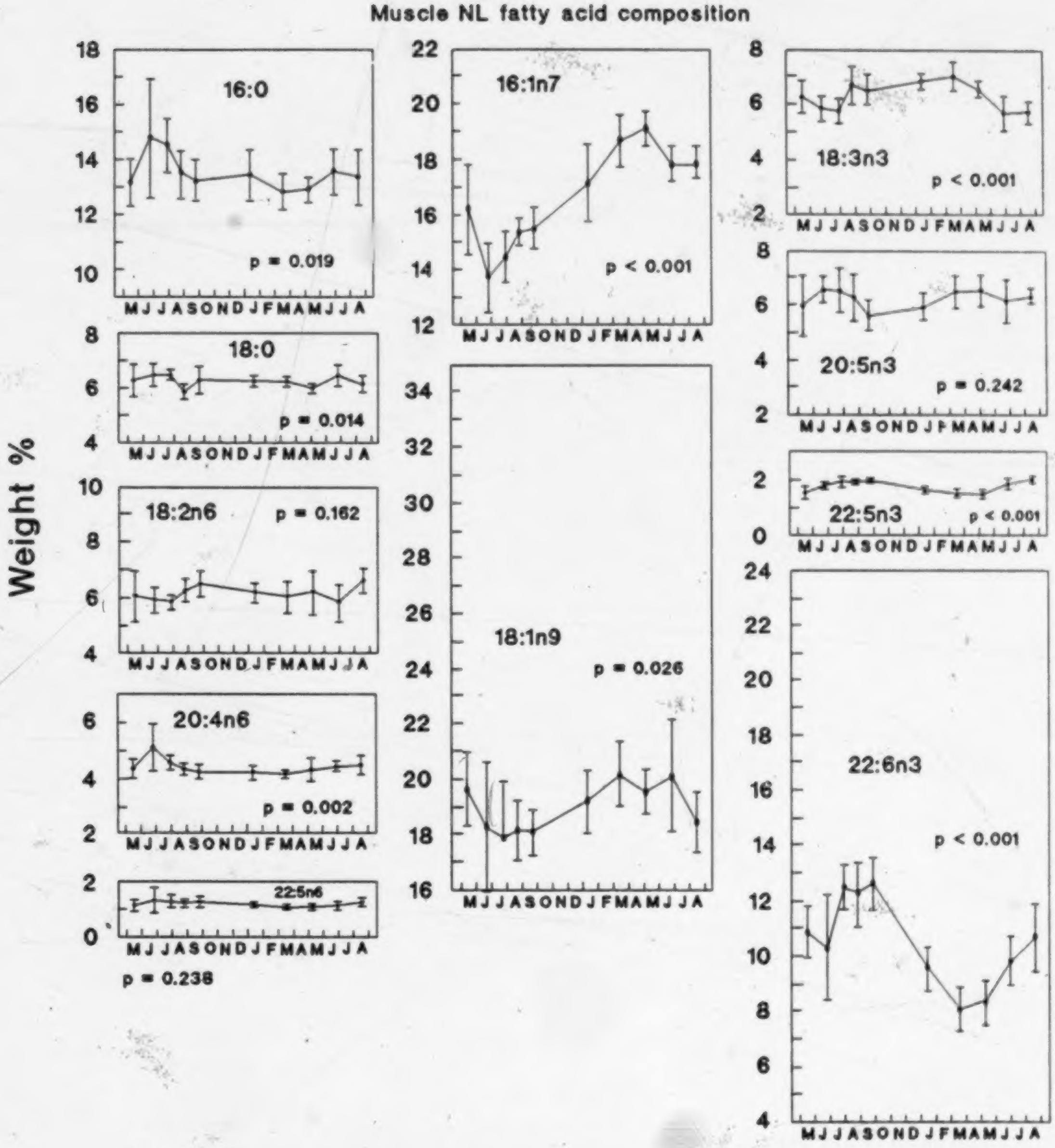


Figure III-10. Seasonal changes in the percentages of individual fatty acids in neutral lipids of white muscle of pike. Other details as in Figure III-4.

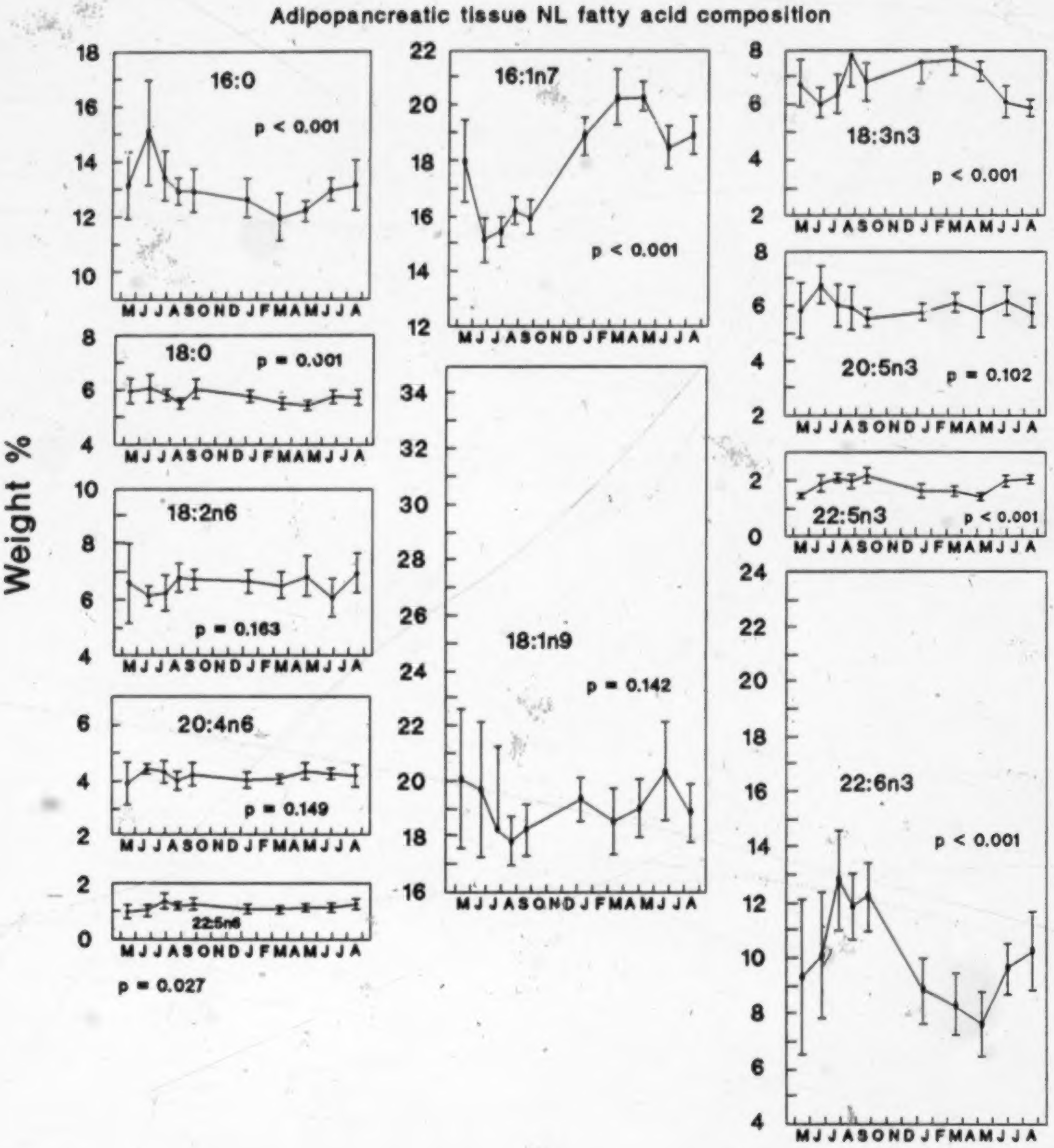


Figure III-11. Seasonal changes in the percentages of individual fatty acids in neutral lipids of adipopancreatic tissue of pike. Details as in Figure III-4.

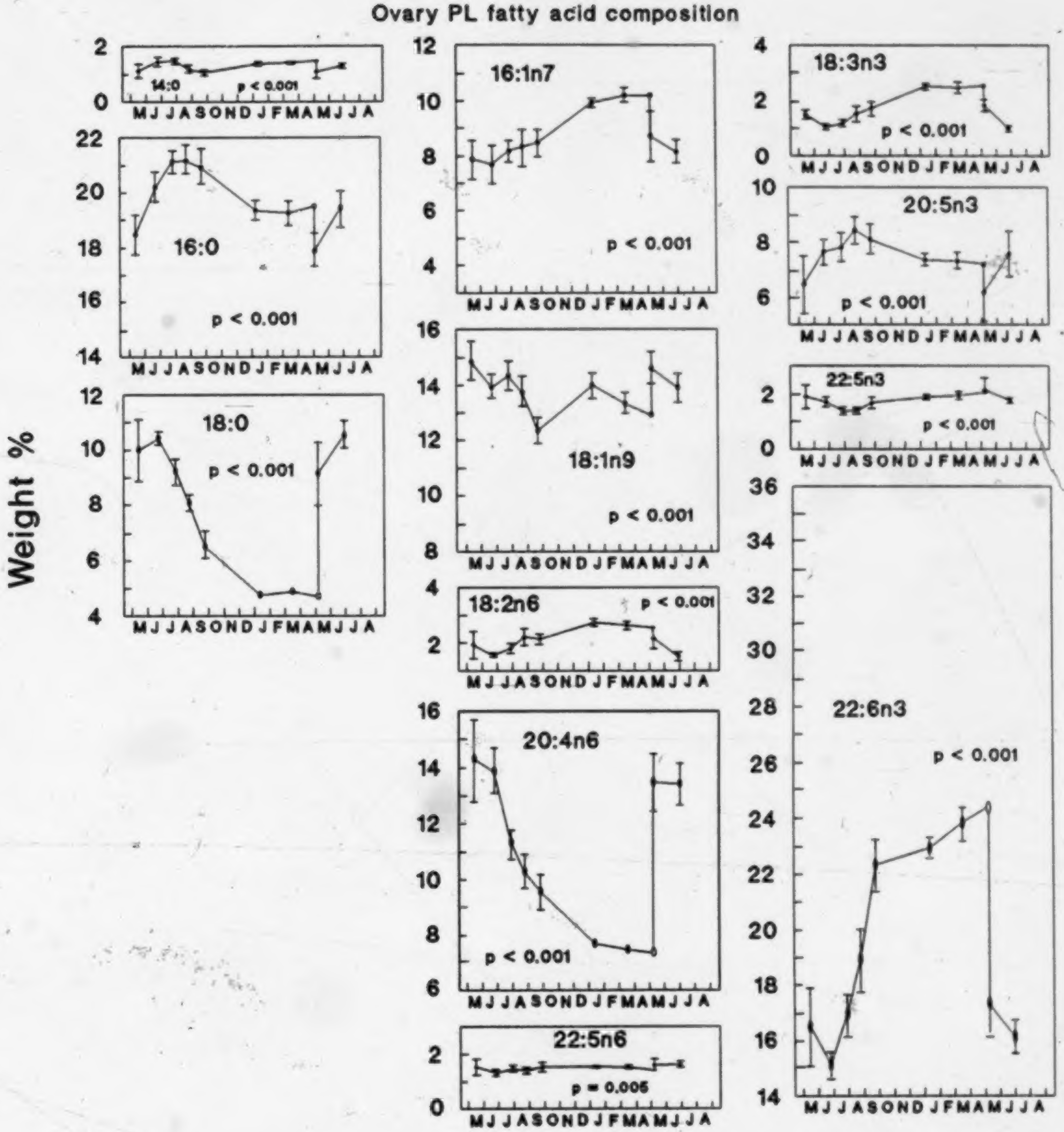


Figure III-12. Seasonal changes in the percentages of individual fatty acids in polar lipids of ovaries of pike. Other details as in Figure III-4.

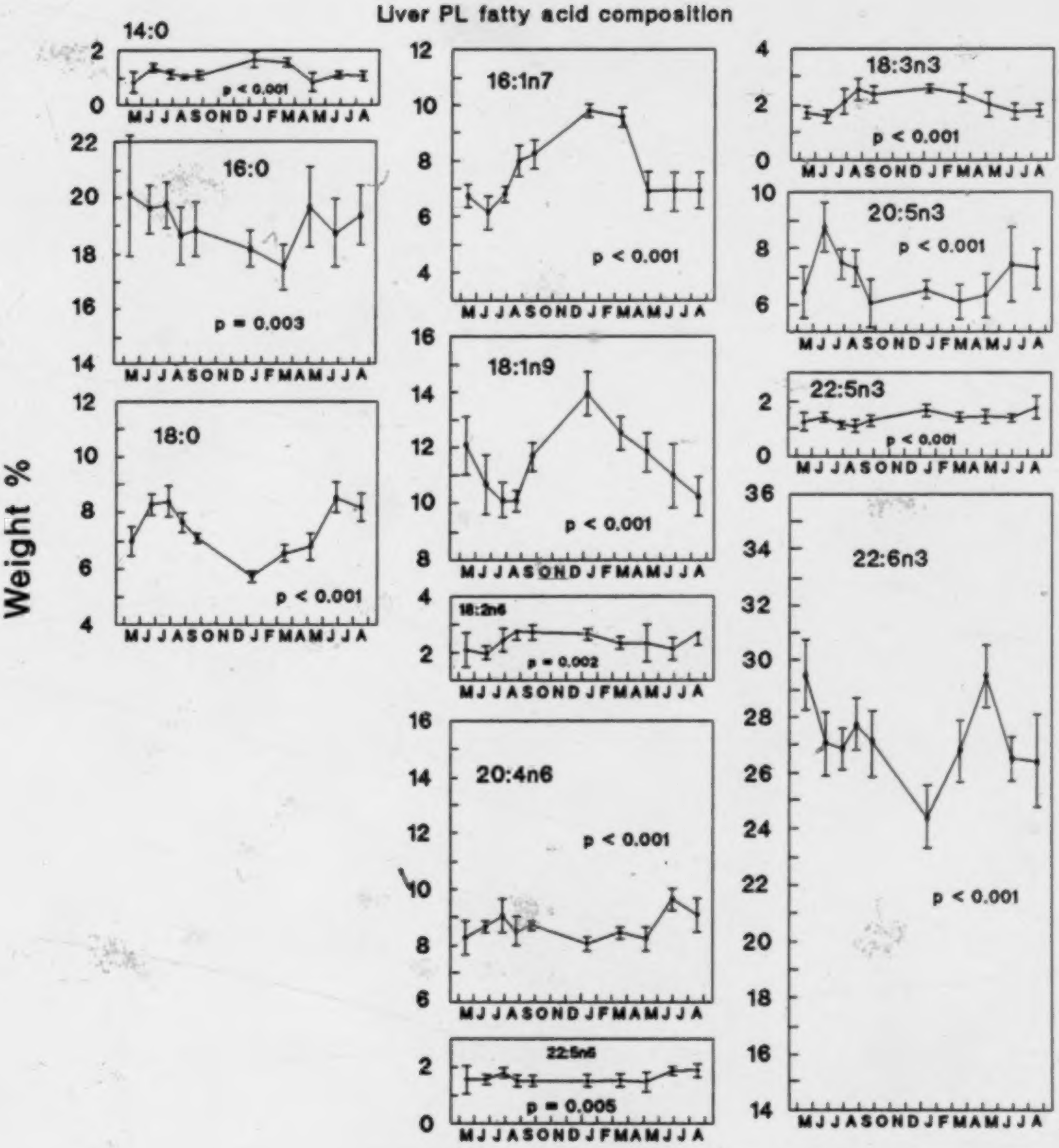


Figure III-13. Seasonal changes in the percentages of individual fatty acids in polar lipids of liver of pike. Other details as in Figure III-4.

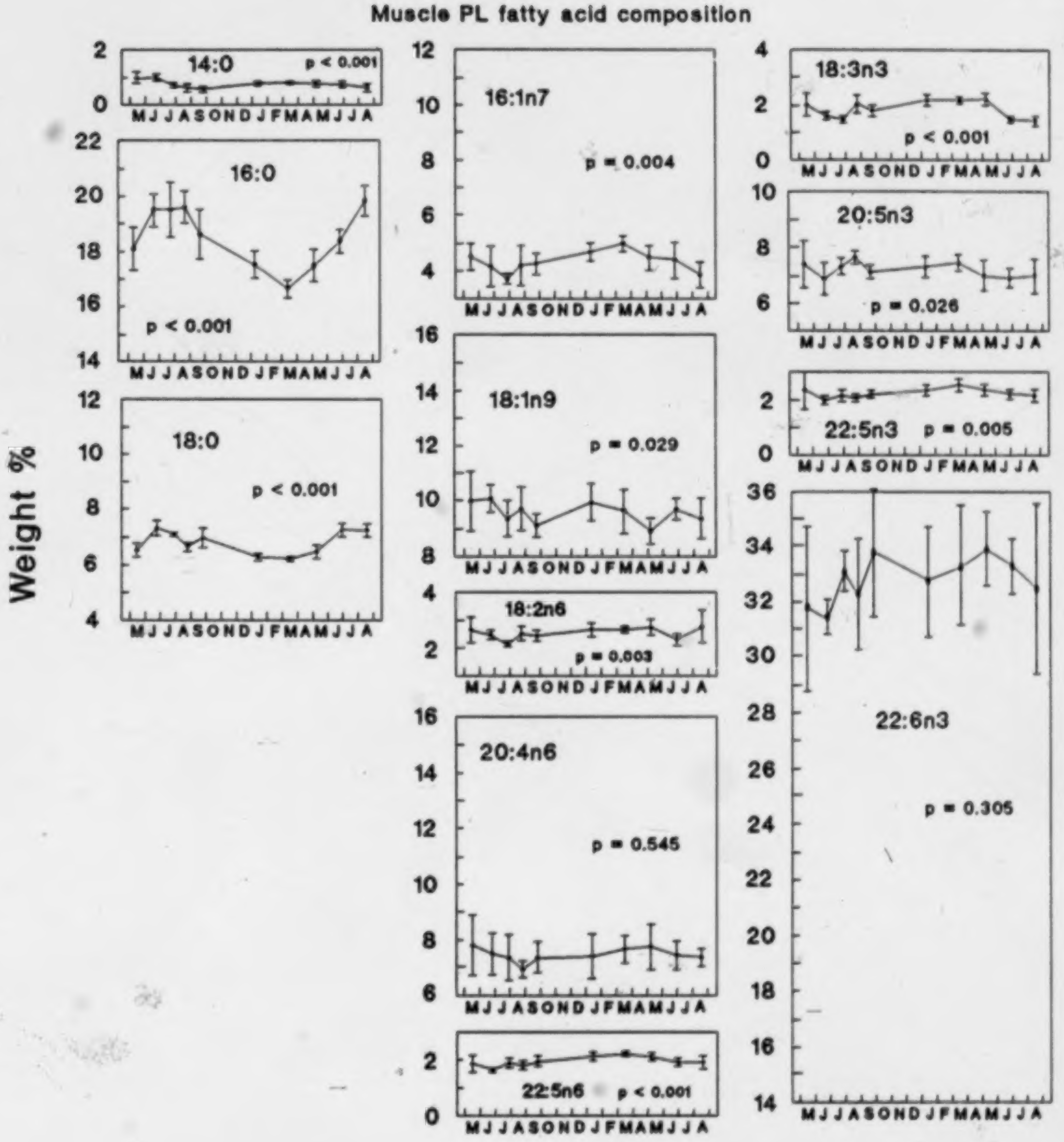


Figure III-14. Seasonal changes in the percentages of individual fatty acids in polar lipids of white muscle of pike. Other details as in Figure III-4.

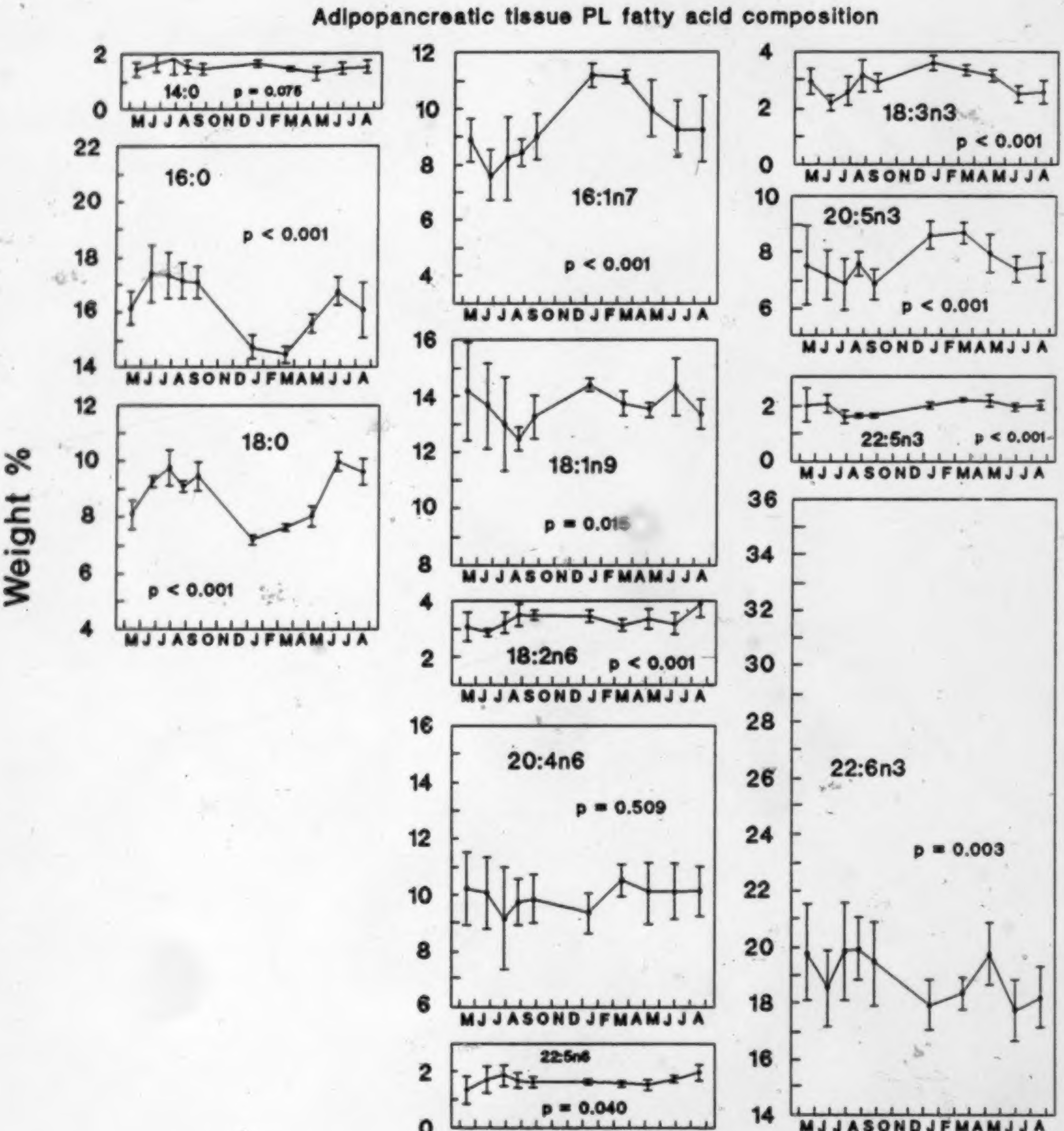


Figure III-15. Seasonal changes in the percentages of individual fatty acids in polar lipids of adipopancreatic tissue of pike. Details as in Figure III-4.

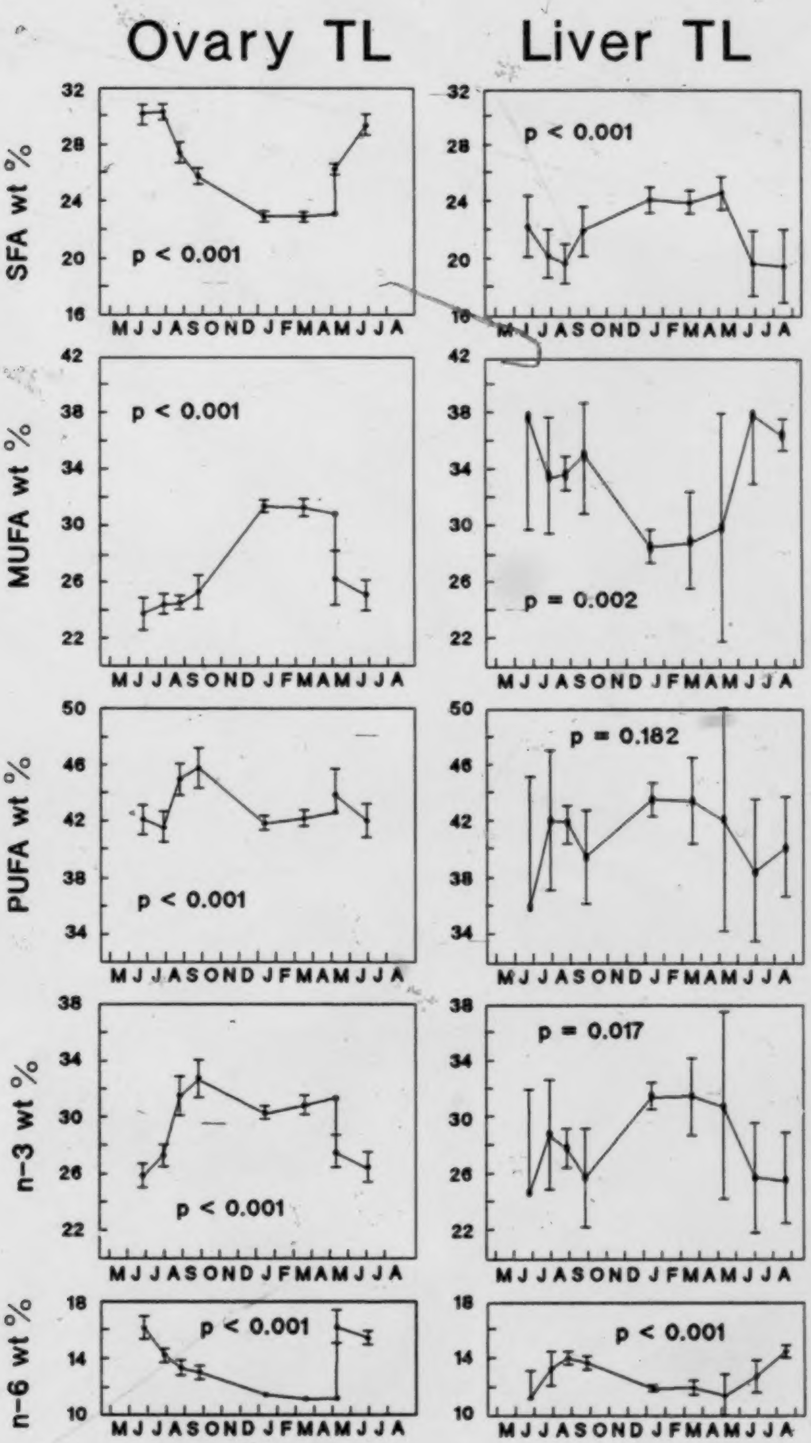
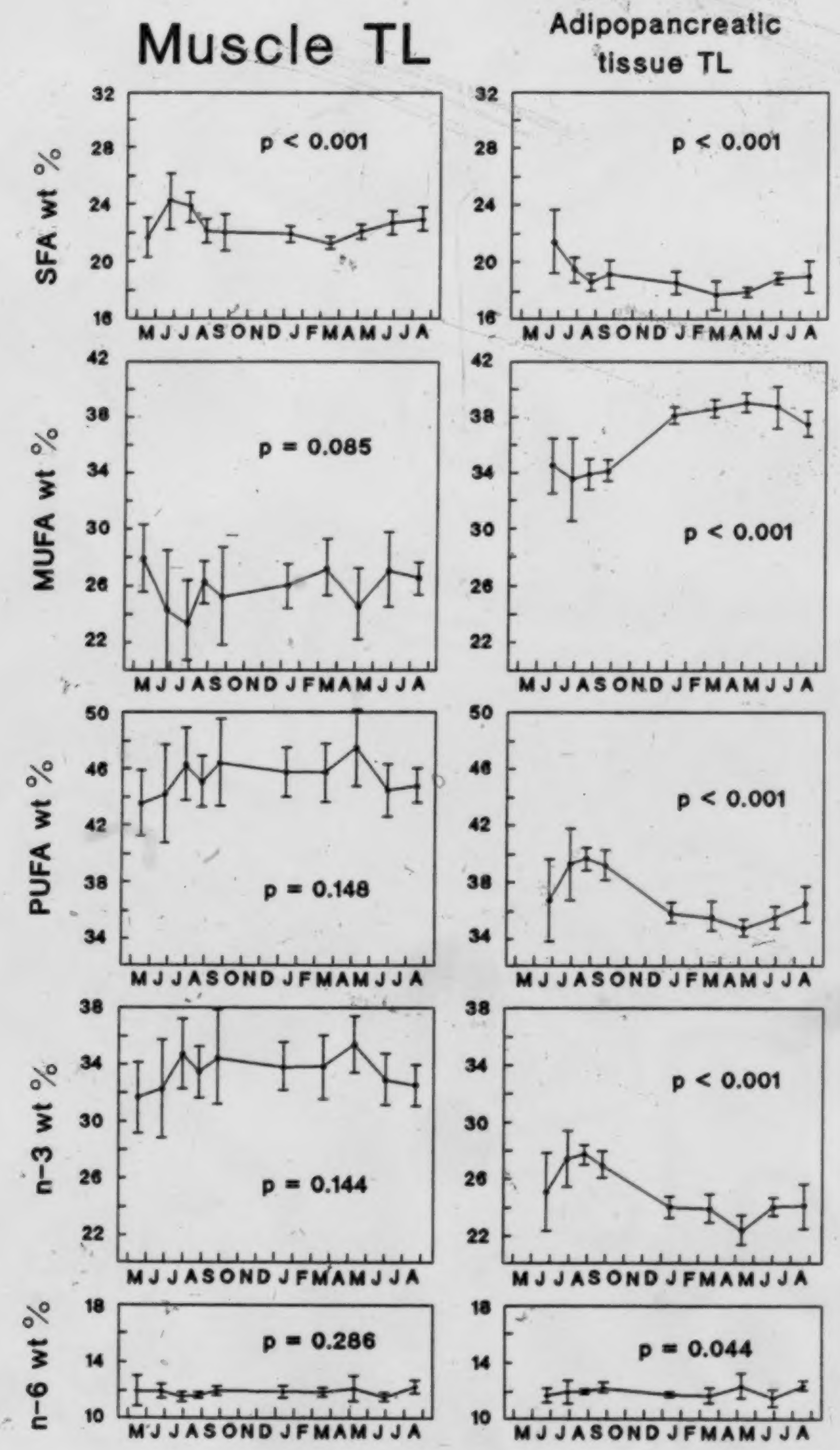


Figure III-16. Seasonal changes in the percentages of major fatty acid groups in total lipids (TL) (ie: NL and PL combined) of ovary and liver of pike. n values are given in Table III-1. Other details as in Figure III-4.



Muscle TL

Adipopancreatic tissue TL

Figure III-17. Seasonal changes in the percentages of major fatty acid groups in total lipids (TL) (ie: NL and PL combined) of white muscle and adipopancreatic tissue of pike. n values are given in Table III-1. Details as in Figure III-4.

Table III-1. Seasonal changes in the fatty acid composition of total lipids in tissues of female northern pike. Standard errors for these data are given in Appendix 3.

			Ovary										
		Seasonal[d]	1987					1988					
Fatty Acid	p Value[c]	Range wt %	May	June[b] 6	July 6	August 7	Sept. 7	Jan. 7	March 7	May[f] 2	May[g] 4	June 8	Aug.
16:0	<0.001	3.7	-----	19.2[a]	20.2	19.3	18.6	16.6	16.5	16.8	16.8	18.5	----
18:0	<0.001	4.7	-----	9.8	8.9	7.2	6.3	5.3	5.5	5.2	8.6	9.9	----
16:1n7	<0.001	3.9	-----	8.7	9.3	10.0	10.1	12.1	12.6	12.5	10.2	9.9	----
18:1n9	<0.001	4.9	-----	15.0	15.0	14.5	15.1	19.4	18.7	18.3	16.1	15.1	----
18:2n6	<0.001	1.5	-----	2.4	2.5	2.9	3.2	3.8	3.7	3.7	2.7	2.3	----
20:4n6	<0.001	6.3	-----	12.4	10.2	9.0	8.3	6.3	6.1	6.3	11.9	11.6	----
22:5n6	<0.001	0.4	-----	1.3	1.5	1.4	1.5	1.3	1.3	1.2	1.6	1.6	----
18:3n3	<0.001	1.7	-----	1.5	1.8	2.2	2.4	3.0	3.0	3.2	2.2	1.5	----
20:5n3	<0.001	2.0	-----	7.4	7.6	8.0	7.5	6.1	6.1	6.0	6.2	7.4	----
22:5n3	<0.001	0.6	-----	1.8	1.5	1.5	1.7	1.7	1.7	1.9	2.1	1.8	----
22:6n3	<0.001	6.1	-----	15.1	16.4	19.7	21.2	19.6	20.1	20.3	17.1	15.7	----
others	<0.001	1.0	-----	4.2	3.9	3.2	3.3	3.9	3.7	3.6	3.7	3.7	----
SFA	<0.001	7.4	-----	30.1	30.3	27.4	25.7	22.9	22.9	23.1	26.2	29.3	----
MUFA	<0.001	7.7	-----	23.7	24.4	24.5	25.3	31.4	31.3	30.8	26.3	25.0	----
PUFA	<0.001	4.2	-----	42.0	41.5	44.9	45.7	41.8	42.1	42.6	43.8	41.9	----
all n-6	<0.001	5.0	-----	16.1	14.2	13.3	13.0	11.4	11.2	11.2	16.2	15.4	----
all n-3	<0.001	6.9	-----	25.9	27.3	31.5	32.8	30.4	30.9	31.4	27.6	26.5	----
FA conc. % wet wt.[e]	<0.001	3.29	-----	0.77	0.85	1.29	2.32	3.98	4.06	2.84	0.98	0.83	----

a - fatty acid composition is expressed as the mean weight % of the indicated fatty acids in tissue total lipids.

b - sample sizes are given directly below each sampling date.

c - p values show the statistical significance of seasonal variation for each variable as tested using one-way ANOVA.

d - seasonal range refers to the difference between the highest and lowest monthly mean recorded for that variable over the fifteen month sampling period.

e - the content of all fatty acids in total lipids was summed and expressed as a percentage of tissue wet weight

f - data for pike which had not spawned and still contained mature eggs.

g - data for pike which had spawned all their eggs.

Table III-1. continued... Seasonal changes in the fatty acid composition of total lipids in pike tissues.

			Liver									
		Seasonal[d]	1987					1988				
Fatty Acid	p Value[c]	Range wt %	May	June[b] 6	July 6	August 7	Sept. 5	Jan. 7	March 7	May 7	June 8	Aug. 6
16:0	<0.001	5.1	-----	15.2[a]	13.2	12.5	14.0	16.9	16.0	17.6	12.9	12.6
18:0	0.020	1.5	-----	6.9	6.9	6.9	7.5	6.0	6.8	6.6	6.5	6.7
16:1n7	0.136	2.0	-----	12.8	11.6	12.5	12.7	11.5	12.2	11.4	13.4	13.2
18:1n9	<0.001	8.0	-----	24.9	22.0	21.3	22.4	17.1	16.9	18.6	24.4	23.2
18:2n6	<0.001	3.8	-----	4.8	6.3	7.2	6.2	3.4	3.4	3.7	5.3	7.2
20:4n6	<0.001	1.8	-----	5.5	5.8	5.7	6.4	7.2	7.3	6.6	6.1	6.1
22:5n6	0.004	0.4	-----	0.9	1.3	1.2	1.1	1.3	1.3	1.1	1.3	1.3
18:3n3	<0.001	2.5	-----	3.0	4.2	5.2	3.9	2.9	3.0	2.7	3.2	3.4
20:5n3	0.022	2.1	-----	7.2	6.9	5.9	5.1	6.0	5.5	5.5	6.6	6.8
22:5n3	<0.001	1.3	-----	2.0	2.2	1.7	1.2	1.5	1.3	1.2	2.1	2.5
22:6n3	<0.001	9.2	-----	12.6	15.6	15.1	15.5	21.2	21.8	21.4	13.9	13.0
others	<0.001	1.5	-----	3.9	3.9	4.6	3.5	3.7	3.5	3.1	3.9	3.8
SFA	<0.001	5.2	-----	22.3	20.3	19.7	22.0	24.2	24.0	24.7	19.7	19.5
MUFA	0.002	9.3	-----	37.8	33.6	33.8	35.0	28.6	29.0	29.9	37.9	36.4
PUFA	0.182	7.6	-----	36.0	42.2	42.0	39.5	43.6	43.5	42.3	38.6	40.2
all n-6	<0.001	3.2	-----	11.3	13.3	14.1	13.7	12.0	12.0	11.4	12.8	14.5
all n-3	0.017	6.8	-----	24.8	28.9	27.9	25.8	31.6	31.5	30.8	25.8	25.7
FA conc. % wet wt.[e]	<0.001	5.84	-----	7.98	6.24	5.48	4.15	2.14	2.15	2.78	6.09	6.05

a - fatty acid composition is expressed as the mean weight % of the indicated fatty acids in tissue total lipids.

b - sample sizes are given directly below each sampling date.

c - p values show the statistical significance of seasonal variation for each variable as tested using one-way ANOVA.

d - seasonal range refers to the difference between the highest and lowest monthly mean recorded for that variable over the fifteen month sampling period.

e - the content of all fatty acids in total lipids was summed and expressed as a percentage of tissue wet weight

Table III-1. continued... Seasonal changes in the fatty acid composition of total lipids in pike tissues.

			Muscle									
		Seasonal[d]	1987					1988				
Fatty Acid	p Value[c]	Range wt %	May 5	June[b] 6	July 6	August 7	Sept. 6	Jan. 6	March 7	May 7	June 7	Aug. 6
16:0	<0.001	2.4	15.0[a]	17.1	16.9	15.8	15.3	15.4	14.7	15.5	15.7	16.1
18:0	<0.001	0.7	6.3	6.8	6.7	6.1	6.5	6.2	6.2	6.2	6.8	6.6
16:1n7	0.020	2.6	11.8	9.6	9.5	11.2	10.9	11.2	12.1	11.0	11.7	11.9
18:1n9	0.161	2.4	16.1	14.8	13.9	15.0	14.3	14.8	15.2	13.7	15.4	14.6
18:2n6	0.066	0.9	4.9	4.4	4.1	4.9	4.8	4.5	4.4	4.2	4.2	5.0
20:4n6	0.036	0.9	5.6	6.1	5.8	5.3	5.5	5.7	5.8	6.2	5.8	5.7
22:5n6	0.013	0.2	1.4	1.4	1.6	1.4	1.6	1.6	1.6	1.6	1.5	1.5
18:3n3	0.006	1.1	4.7	3.9	3.8	4.9	4.6	4.6	4.7	4.2	3.8	3.9
20:5n3	0.099	0.7	6.5	6.7	7.0	6.8	6.3	6.6	7.0	6.8	6.6	6.6
22:5n3	0.143	0.2	1.9	1.9	2.0	2.0	2.1	2.0	2.0	2.0	2.0	2.1
22:6n3	0.379	3.9	18.6	19.7	22.0	19.7	21.6	20.7	20.3	22.5	20.5	20.0
others	<0.001	1.5	6.9	7.2	6.4	6.6	6.3	6.4	5.8	5.7	5.8	5.8
SFA	<0.001	3.0	21.7	24.3	23.9	22.1	22.1	22.0	21.3	22.1	22.7	22.9
MUFA	0.085	4.5	27.9	24.3	23.4	26.2	25.2	26.0	27.2	24.7	27.1	26.5
PUFA	0.148	4.0	43.5	44.1	46.3	45.0	46.4	45.7	45.7	47.5	44.4	44.7
all n-6	0.286	0.7	11.9	11.9	11.5	11.6	11.9	11.8	11.8	12.0	11.5	12.2
all n-3	0.144	3.7	31.7	32.3	34.8	33.5	34.5	33.9	33.9	35.4	32.9	32.6
FA conc. % wet wt.[e]	0.081	0.43	0.93	0.76	0.71	0.97	1.12	0.83	0.84	0.69	0.78	0.73

a - fatty acid composition is expressed as the mean weight % of the indicated fatty acids in tissue total lipids.

b - sample sizes are given directly below each sampling date.

c - p values show the statistical significance of seasonal variation for each variable as tested using one-way ANOVA.

d - seasonal range refers to the difference between the highest and lowest monthly mean recorded for that variable over the fifteen month sampling period.

e - the content of all fatty acids in total lipids was summed and expressed as a percentage of tissue wet weight

Table III-1. continued... Seasonal changes in the fatty acid composition of total lipids in pike tissues.

			Adipopancreatic Tissue									
				1987				1988				
Fatty Acid	p Value[c]	Seasonal[d] Range wt %	May	June[b] 7	July 6	August 7	Sept. 7	Jan. 7	March 7	May 7	June 8	Aug. 6
16:0	<0.001	3.1	-----	15.1[a]	13.5	13.0	13.0	12.6	12.0	12.3	13.0	13.1
18:0	<0.001	0.6	-----	6.1	5.9	5.6	6.1	5.8	5.6	5.5	5.8	5.8
16:1n7	<0.001	5.1	-----	15.0	15.3	16.1	15.9	18.8	20.1	20.1	18.4	18.8
18:1n9	0.162	2.5	-----	19.5	18.3	17.8	18.2	19.3	18.5	18.9	20.3	18.8
18:2n6	0.047	0.8	-----	6.1	6.2	6.8	6.7	6.6	6.4	6.8	6.1	6.9
20:4n6	0.104	0.5	-----	4.5	4.3	4.0	4.2	4.0	4.1	4.4	4.3	4.2
22:5n6	0.050	0.3	-----	1.0	1.4	1.2	1.3	1.1	1.1	1.1	1.1	1.3
18:3n3	<0.001	1.8	-----	6.0	6.3	7.7	6.8	7.5	7.5	7.1	6.1	5.9
20:5n3	0.043	1.2	-----	6.8	6.1	6.0	5.6	5.9	6.2	5.9	6.2	5.8
22:5n3	<0.001	0.8	-----	1.9	2.1	1.9	2.2	1.6	1.6	1.4	2.0	2.0
22:6n3	<0.001	5.0	-----	10.4	13.0	12.0	12.4	9.0	8.6	8.0	9.8	10.3
others	0.006	1.4	-----	7.5	7.7	8.0	7.7	7.7	8.3	8.5	7.1	7.1
SFA	<0.001	3.7	-----	21.3	19.4	18.5	19.1	18.4	17.6	17.8	18.8	18.9
MUFA	<0.001	5.4	-----	34.5	33.6	33.9	34.1	38.1	38.6	39.0	38.7	37.6
PUFA	<0.001	2.9	-----	36.7	39.3	39.6	39.2	35.8	35.6	34.7	35.5	36.4
all n-6	0.044	0.9	-----	11.6	11.9	11.9	12.2	11.8	11.7	12.3	11.5	12.4
all n-3	<0.001	5.3	-----	25.0	27.4	27.7	26.9	24.0	23.9	22.4	24.0	24.0
FA conc. % wet wt.[e]	0.250	16.8	40.2	56.9	57.4	57.4	53.4	57.5	49.2	45.3	62.1	61.4

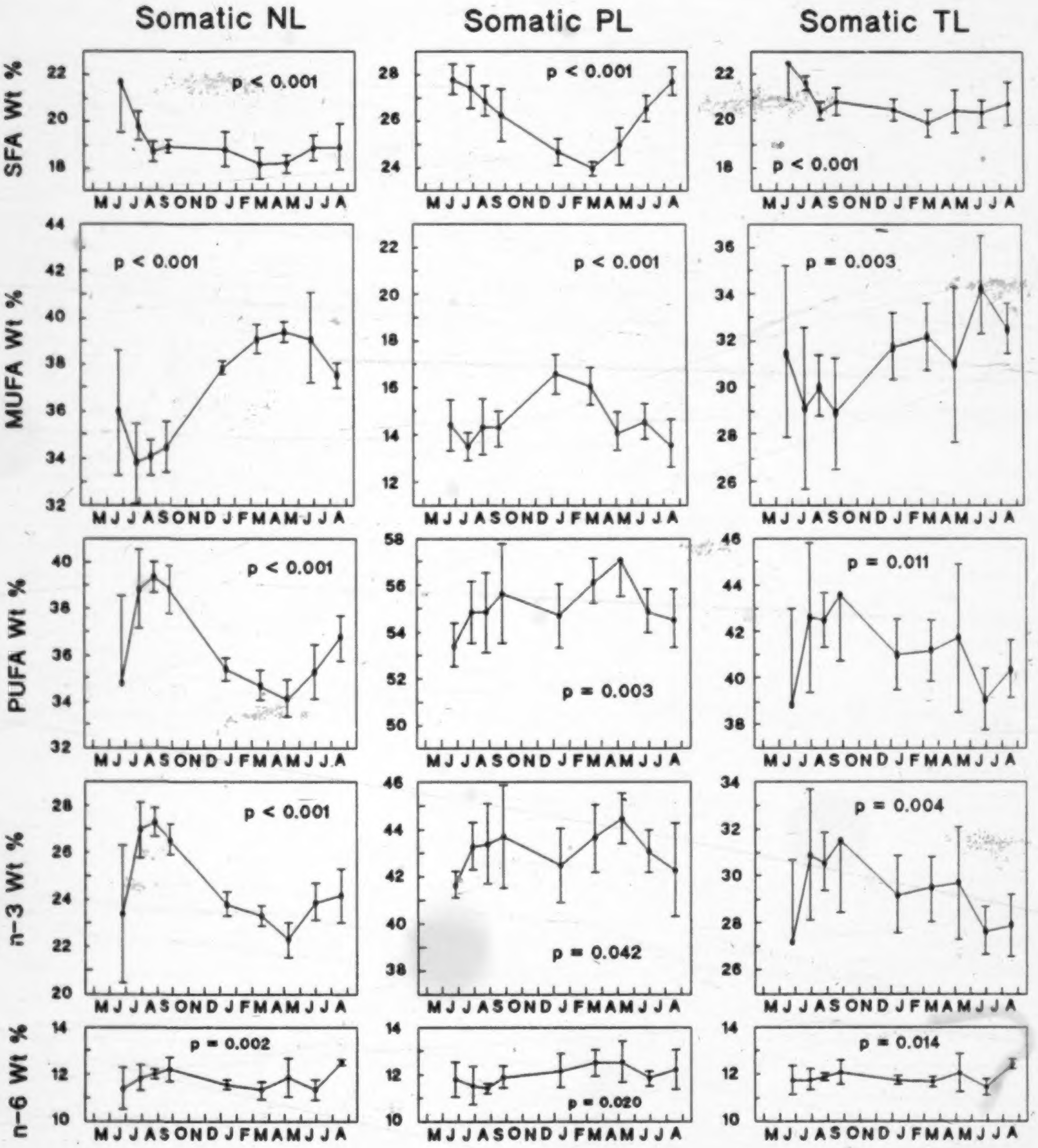
a - fatty acid composition is expressed as the mean weight % of the indicated fatty acids in tissue total lipids.

b - sample sizes are given directly below each sampling date.

c - p values show the statistical significance of seasonal variation for each variable as tested using one-way ANOVA.

d - seasonal range refers to the difference between the highest and lowest monthly mean recorded for that variable over the fifteen month sampling period.

e - the content of all fatty acids in total lipids was summed and expressed as a percentage of tissue wet weight



Somatic NL

Somatic PL

Somatic TL

Figure III-18. Seasonal changes in the percentages of major fatty acid groups in the combined NL's, PL's, and TL's of the three somatic tissues. Samples sizes are given in Tables III-2,3,8. Other details as in Figure III-4.

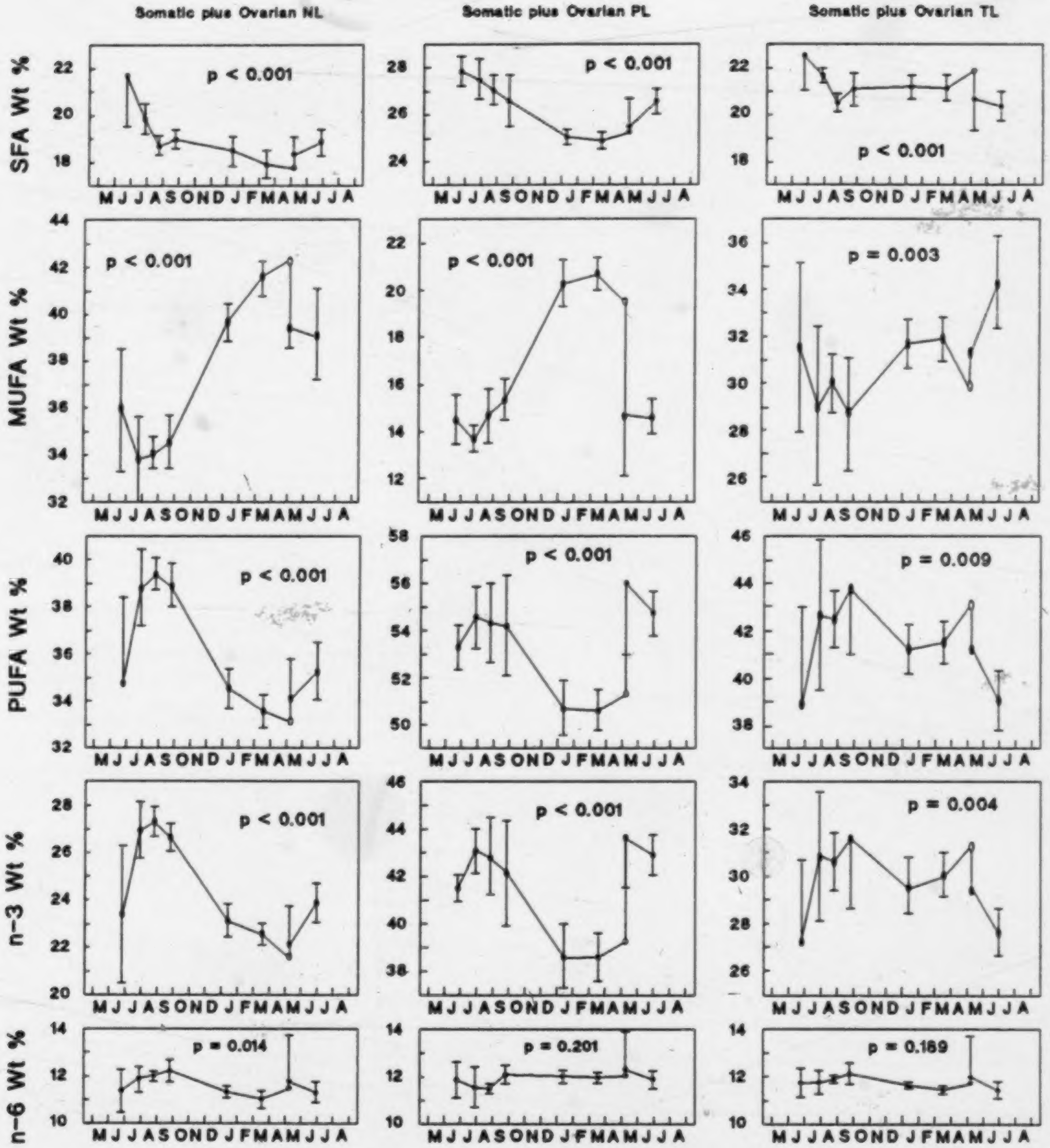


Figure III-19. Seasonal changes in the percentages of major fatty acid groups in the combined NL, PL, and TL of the ovarian and somatic tissues of pike. Sample sizes are given in Tables III-4,5,7. Other details as in Figure III-4.

Table III-2. Seasonal changes in the fatty acid composition of the combined neutral lipids from the three somatic tissues of female northern pike. Standard errors for these data are given in Appendix 4. Other details as in Table III-1.

		Seasonal	1987					1988				
Fatty Acid	p Value	Range wt %	May	June 6	July 6	August 7	Sept. 4	Jan. 6	March 7	May 7	June 7	Aug. 6
16:0	<0.001	3.1	-----	15.4[a]	13.7	13.0	12.8	12.9	12.3	12.5	12.9	13.0
18:0	<0.001	0.6	-----	6.3	6.1	5.7	6.2	5.9	5.9	5.7	5.9	5.9
16:1n7	<0.001	5.2	-----	14.8	14.8	15.7	15.8	18.3	19.6	20.0	18.0	18.2
18:1n9	0.018	2.8	-----	21.2	19.0	18.4	18.7	19.7	19.5	19.4	21.1	19.4
18:2n6	0.002	1.1	-----	5.9	6.2	6.7	6.7	6.5	6.3	6.5	5.9	7.0
20:4n6	0.017	0.5	-----	4.5	4.4	4.1	4.2	4.0	4.0	4.2	4.3	4.3
22:5n6	0.002	0.3	-----	1.0	1.3	1.2	1.3	1.1	1.1	1.1	1.1	1.2
18:3n3	<0.001	1.8	-----	5.5	6.0	7.3	6.5	7.3	7.3	6.9	5.8	5.7
20:5n3	0.131	0.9	-----	6.5	6.3	6.2	5.6	5.8	6.2	6.1	6.3	6.1
22:5n3	<0.001	0.7	-----	1.8	2.1	1.9	2.1	1.6	1.6	1.4	2.0	2.1
22:6n3	<0.001	4.3	-----	9.6	12.5	12.0	12.4	9.0	8.2	7.9	9.8	10.3
others	<0.001	1.4	-----	7.5	7.5	7.9	7.7	7.9	8.0	8.2	6.8	6.8
SFA	<0.001	3.5	-----	21.7	19.8	18.7	19.0	18.8	18.2	18.2	18.9	18.9
MUFA	<0.001	5.6	-----	36.0	33.8	34.1	34.5	37.9	39.1	39.4	39.1	37.6
PUFA	<0.001	5.2	-----	34.8	38.8	39.3	38.8	35.4	34.7	34.1	35.2	36.7
all n-6	0.002	1.2	-----	11.4	11.9	12.0	12.2	11.6	11.4	11.9	11.3	12.5
all n-3	<0.001	5.0	-----	23.4	27.0	27.3	26.6	23.8	23.4	22.3	23.9	24.1
FA conc. % wet wt.[b]	0.241	0.7	-----	1.7	1.2	1.5	1.3	1.2	1.1	1.0	1.6	1.3

a - fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in the combined NL's from the three somatic tissues which were analyzed.

b - the content of all fatty acids in the combined neutral lipids of the three somatic tissues was summed and expressed as a percentage of tissue wet weight

Table III-3. Seasonal changes in the fatty acid composition of the combined polar lipids from the three somatic tissues of female northern pike. Standard errors for these data are given in Appendix 5. Other details as in Table III-1.

			1987					1988				
Fatty Acid	p Value	Seasonal Range wt %	May	June 6	July 6	August 7	Sept. 6	Jan. 6	March 7	May 7	June 8	Aug. 6
16:0	<0.001	3.0	-----	19.4[a]	19.5	19.5	18.6	17.6	16.7	17.7	18.4	19.7
18:0	<0.001	1.2	-----	7.4	7.2	6.7	7.0	6.2	6.3	6.5	7.4	7.3
16:1n7	<0.001	1.9	-----	4.3	4.0	4.6	4.8	5.8	5.9	4.8	4.6	4.2
18:1n9	<0.001	1.5	-----	10.1	9.5	9.8	9.5	10.8	10.2	9.3	9.9	9.5
18:2n6	0.003	0.7	-----	2.4	2.1	2.5	2.5	2.7	2.6	2.7	2.3	2.8
20:4n6	0.427	0.8	-----	7.8	7.5	7.1	7.6	7.6	7.9	7.8	7.7	7.6
22:5n6	<0.001	0.5	-----	1.6	1.9	1.8	1.9	2.0	2.1	2.0	1.9	1.9
18:3n3	<0.001	0.9	-----	1.6	1.5	2.1	1.9	2.3	2.2	2.2	1.5	1.4
20:5n3	0.027	0.7	-----	7.0	7.3	7.6	7.0	7.2	7.2	6.9	6.9	7.0
22:5n3	0.006	0.3	-----	2.0	2.1	2.0	2.1	2.2	2.3	2.2	2.1	2.1
22:6n3	0.246	2.2	-----	31.2	32.5	31.7	32.8	30.9	31.9	33.1	32.5	31.8
others	<0.001	0.6	-----	4.4	4.2	3.9	3.8	4.0	3.8	3.9	4.0	4.1
SFA	<0.001	3.8	-----	27.8	27.4	26.9	26.3	24.7	24.0	25.0	26.5	27.7
MUFA	<0.001	3.1	-----	14.4	13.5	14.3	14.3	16.6	16.1	14.1	14.6	13.6
PUFA	0.003	3.7	-----	53.4	54.8	54.8	55.6	54.7	56.2	57.1	54.9	54.5
all n-6	0.020	1.2	-----	11.8	11.5	11.4	11.9	12.2	12.5	12.6	11.8	12.2
all n-3	0.042	2.9	-----	41.6	43.3	43.4	43.7	42.5	43.7	44.5	43.1	42.3
FA conc. % wet wt.[b]	<0.001	0.14	-----	0.34	0.33	0.36	0.43	0.47	0.46	0.41	0.36	0.33

a - Fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in the combined PL's from the three somatic tissues which were analyzed.

b - the content of all fatty acids in the combined neutral lipids of the three somatic tissues was summed and expressed as a percentage of tissue wet weight

Table III-4. Seasonal changes in the fatty acid composition of the combined neutral lipids from the ovarian and somatic tissues of female northern pike. Standard errors for these data are given in Appendix 6. Other details as in Table III-1.

			1987					1988					
Fatty Acid	p Value	Seasonal Range wt %	May	June 6	July 6	August 7	Sept. 4	Jan. 6	March 7	May[c] 2	May[d] 4	June 7	Aug.
16:0	<0.001	3.6	-----	15.4[a]	13.7	13.0	12.8	12.4	11.8	11.8	12.7	12.9	----
18:0	<0.001	0.6	-----	6.3	6.1	5.7	6.2	6.1	6.1	6.0	5.7	5.9	----
16:1n7	<0.001	5.0	-----	14.8	14.8	15.7	15.8	18.1	19.4	19.4	19.8	18.0	----
18:1n9	<0.001	4.6	-----	21.2	19.0	18.4	18.7	21.5	22.3	23.0	19.7	21.1	----
18:2n6	0.033	0.8	-----	5.9	6.2	6.7	6.7	6.5	6.3	6.4	6.5	5.9	----
20:4n6	<0.001	0.7	-----	4.5	4.4	4.1	4.2	3.8	3.8	4.1	4.2	4.3	----
22:5n6	<0.001	0.3	-----	1.0	1.3	1.2	1.3	1.0	1.0	1.0	1.1	1.1	----
18:3n3	<0.001	1.7	-----	5.5	6.0	7.2	6.4	6.9	6.6	6.3	6.6	5.8	----
20:5n3	<0.001	1.1	-----	6.5	6.3	6.2	5.6	5.4	5.5	5.4	6.0	6.3	----
22:5n3	<0.001	0.8	-----	1.8	2.1	1.9	2.1	1.5	1.5	1.3	1.4	2.0	----
22:6n3	<0.001	4.4	-----	9.6	12.6	12.0	12.6	9.4	8.9	8.6	8.2	9.9	----
others	0.015	1.4	-----	7.5	7.5	7.8	7.6	7.2	6.9	6.7	8.1	6.8	----
SFA	<0.001	3.9	-----	21.7	19.8	18.7	19.0	18.5	17.9	17.8	18.4	18.9	----
MUFA	<0.001	8.5	-----	36.0	33.8	34.1	34.5	39.7	41.6	42.3	39.5	39.1	----
PUFA	<0.001	6.2	-----	34.8	38.8	39.4	38.9	34.6	33.6	33.2	34.0	35.2	----
all n-6	0.014	1.2	-----	11.4	11.9	12.0	12.2	11.4	11.0	11.5	11.8	11.3	----
all n-3	<0.001	5.6	-----	23.4	27.0	27.3	26.7	23.2	22.6	21.7	22.2	23.9	----
FA conc. % wet wt.[b]	0.285	1.0	-----	1.7	1.2	1.5	1.2	1.2	1.1	0.7	1.0	1.5	----

a - Fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in the combined NL's from the ovarian and somatic tissues which were analyzed.

b - the content of all fatty acids in the combined neutral lipids of the three somatic tissues was summed and expressed as a percentage of tissue wet weight

c - data for pike which had not spawned and still contained mature eggs

d - data for pike which had spawned all their eggs

Table III-5. Seasonal changes in the fatty acid composition of the combined polar lipids from the ovarian and somatic tissues of female northern pike. Standard errors for these data are given in Appendix 7. Other details as in Table III-1.

Fatty Acid	p Value	Seasonal Range wt %	1987					1988					
			May	June 6	July 6	August 7	Sept. 6	Jan. 6	March 7	May[c] 2	May[d] 4	June 8	Aug.
16:0	<0.001	1.6	-----	19.4[a]	19.5	19.5	19.0	18.5	18.3	18.9	17.9	18.4	----
18:0	<0.001	2.1	-----	7.4	7.2	6.8	6.9	5.4	5.4	5.3	6.7	7.4	----
16:1n7	<0.001	4.5	-----	4.3	4.1	4.7	5.4	7.8	8.6	8.0	5.0	4.7	----
18:1n9	<0.001	2.9	-----	10.1	9.6	10.0	10.0	12.5	12.2	11.5	9.7	10.0	----
18:2n6	<0.001	0.6	-----	2.4	2.1	2.5	2.4	2.7	2.6	2.6	2.6	2.3	----
20:4n6	0.558	0.6	-----	7.8	7.6	7.3	7.9	7.6	7.6	7.8	7.8	7.7	----
22:5n6	0.002	0.4	-----	1.6	1.9	1.7	1.8	1.8	1.7	1.6	2.0	1.9	----
18:3n3	<0.001	0.9	-----	1.6	1.5	2.1	1.8	2.4	2.4	2.4	2.1	1.5	----
20:5n3	0.002	0.9	-----	7.0	7.3	7.7	7.1	7.3	7.3	7.1	6.8	6.9	----
22:5n3	0.056	0.3	-----	2.0	2.0	2.0	2.0	2.0	2.1	2.1	2.3	2.1	----
22:6n3	<0.001	5.6	-----	31.0	32.2	31.2	31.2	27.0	26.9	27.6	32.5	32.3	----
others	<0.001	0.6	-----	4.4	4.2	3.9	3.8	4.0	3.8	3.8	3.8	4.0	----
SFA	<0.001	2.9	-----	27.8	27.5	27.0	26.6	25.0	24.9	25.3	25.5	26.6	----
MUFA	<0.001	7.0	-----	14.5	13.7	14.7	15.4	20.3	20.7	19.5	14.7	14.6	----
PUFA	<0.001	5.4	-----	53.3	54.6	54.3	54.3	50.7	50.6	51.4	56.0	54.8	----
all n-6	0.201	0.9	-----	11.9	11.6	11.5	12.1	12.1	12.0	12.1	12.4	11.9	----
all n-3	<0.001	5.0	-----	41.5	43.0	42.8	42.2	38.6	38.6	39.3	43.6	42.9	----
FA conc. % wet wt.[b]	<0.001	0.64	-----	0.34	0.33	0.37	0.50	0.82	0.97	0.82	0.41	0.36	----

a - Fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in the combined PL's from the ovarian and somatic tissues which were analyzed.

b - the content of all fatty acids in the combined neutral lipids of the three somatic tissues was summed and expressed as a percentage of tissue wet weight

c - data for pike which had not spawned and still contained mature eggs

d - data for pike which had spawned all their eggs

Table III-6. Seasonal changes in the fatty acid composition of the combined total lipids of the three somatic tissues of female northern pike. Standard errors for these data are given in Appendix 8. Other details as in Table III-1.

Fatty Acid	p value	Seasonal Range wt %	1987					1988				
			May	June 5	July 6	August 7	Sept. 4	Jan. 6	March 7	May 7	June 7	Aug. 6
16:0	<0.001	2.1	-----	15.8[a]	15.1	14.4	14.3	14.2	13.7	14.3	14.0	14.4
18:0	<0.001	0.6	-----	6.5	6.4	5.9	6.4	6.0	6.0	6.0	6.2	6.2
16:1n7	<0.001	3.2	-----	12.9	12.3	13.4	12.8	14.6	15.5	15.0	15.4	15.3
18:1n9	0.015	3.0	-----	18.7	16.8	16.6	16.1	17.1	16.7	16.0	19.0	17.3
18:2n6	0.002	0.9	-----	5.4	5.2	5.8	5.5	5.4	5.2	5.2	5.2	6.1
20:4n6	0.270	0.7	-----	5.2	5.2	4.7	5.1	5.0	5.2	5.4	5.0	5.0
22:5n6	0.017	0.4	-----	1.1	1.4	1.3	1.5	1.3	1.4	1.4	1.3	1.4
18:3n3	<0.001	1.4	-----	4.9	4.9	6.2	5.2	5.9	5.8	5.4	4.9	4.8
20:5n3	0.107	0.7	-----	6.7	6.6	6.5	6.0	6.2	6.5	6.4	6.4	6.3
22:5n3	<0.001	0.4	-----	1.8	2.1	1.9	2.1	1.8	1.8	1.7	2.0	2.1
22:6n3	0.067	4.5	-----	13.7	17.2	16.0	18.2	15.4	15.4	16.2	14.3	14.9
others	0.027	0.9	-----	7.1	6.7	7.0	6.6	6.7	6.7	6.8	6.2	6.2
SFA	<0.001	2.6	-----	22.5	21.6	20.4	20.8	20.5	19.9	20.4	20.4	20.8
MUFA	0.003	5.4	-----	31.5	29.1	30.0	28.9	31.8	32.2	31.0	34.3	32.5
PUFA	0.011	4.7	-----	38.9	42.6	42.5	43.6	41.0	41.2	41.8	39.1	40.4
all n-6	0.014	1.1	-----	11.7	11.8	11.9	12.1	11.8	11.7	12.1	11.4	12.5
all n-3	0.004	4.3	-----	27.2	30.9	30.6	31.5	29.2	29.5	29.7	27.6	28.0
FA conc. % wet wt.[b]	0.596	0.50	-----	1.87	1.56	1.87	1.68	1.67	1.57	1.42	1.92	1.64

[a] - Fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in the combined total lipids of the three somatic tissues which were analyzed.

[b] - the content of all fatty acids in the combined total lipids of the three somatic tissues was summed and expressed as a percentage of tissue wet weight

Table III-7. Seasonal changes in the fatty acid composition of the combined total lipids of the ovarian and somatic tissues of female northern pike. Standard errors for these data are given in Appendix 9. Other details as in Table III-1.

		Seasonal	1987					1988					
Fatty Acid	p Value	Range wt %	May	June 5	July 6	August 7	Sept. 4	Jan. 6	March 7	May[c] 2	May[d] 4	June 7	Aug.
16:0	<0.001	1.8	-----	15.8[a]	15.1	14.4	14.5	14.9	14.8	15.7	14.4	14.0	----
18:0	<0.001	0.9	-----	6.5	6.4	6.0	6.4	5.8	5.8	5.6	6.0	6.2	----
16:1n7	<0.001	3.1	-----	12.9	12.3	13.4	12.7	13.9	14.3	13.2	14.9	15.4	----
18:1n9	0.031	2.9	-----	18.6	16.8	16.6	16.0	17.8	17.5	16.7	16.4	18.9	----
18:2n6	<0.001	1.4	-----	5.4	5.2	5.8	5.4	4.9	4.6	4.4	5.1	5.2	----
20:4n6	0.085	1.3	-----	5.2	5.2	4.8	5.3	5.4	5.6	6.1	5.4	5.0	----
22:5n6	0.017	0.4	-----	1.1	1.4	1.3	1.5	1.3	1.3	1.3	1.4	1.3	----
18:3n3	0.003	1.9	-----	4.9	4.9	6.1	5.0	5.1	4.7	4.2	5.2	4.9	----
20:5n3	0.151	0.6	-----	6.7	6.6	6.5	6.1	6.2	6.3	6.3	6.3	6.4	----
22:5n3	<0.001	0.4	-----	1.8	2.1	1.9	2.1	1.7	1.8	1.7	1.7	2.0	----
22:6n3	0.018	5.3	-----	13.7	17.2	16.0	18.4	16.6	17.3	19.0	16.1	14.3	----
others	<0.001	2.0	-----	7.1	6.7	7.0	6.4	5.9	5.5	5.1	6.7	6.2	----
SFA	<0.001	2.1	-----	22.5	21.7	20.5	21.1	21.2	21.2	21.9	20.7	20.4	----
MUFA	0.003	5.6	-----	31.5	29.0	30.0	28.7	31.7	31.9	29.9	31.3	34.3	----
PUFA	0.009	4.8	-----	38.9	42.6	42.5	43.7	41.2	41.5	43.1	41.3	39.1	----
all n-6	0.189	0.7	-----	11.8	11.8	11.9	12.2	11.7	11.5	11.8	12.0	11.5	----
all n-3	0.004	4.4	-----	27.2	30.8	30.6	31.6	29.6	30.0	31.3	29.4	27.6	----
FA conc. % wet wt.[b]	0.343	0.66	-----	1.86	1.55	1.86	1.71	2.01	2.10	1.53	1.44	1.91	----

a - Fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in the combined total lipids of the ovarian and somatic tissues which were analyzed.

b - the content of all fatty acids in the combined total lipids of the ovarian and somatic tissues was summed and expressed as a percentage of tissue wet weight

c - data for pike which had not spawned and still contained mature eggs

d - data for pike which had spawned all their eggs

Table III-8. Seasonal changes in the content (g / kg carcass weight) of major fatty acid groups in various lipid compartments of female northern pike. Standard errors for these data are given in Appendix 10. Other details as in Table III-1.

Fatty Acid	p Value	1987					1988				
		May	June	July	August	Sept.	Jan.	March	May	June	Aug.
Somatic Tissue Neutral Lipids											
			(6)	(6)	(7)	(4)	(6)	(7)	(7)	(7)	(6)
SFA	0.085	----	2.137	1.403	1.621	1.371	1.345	1.192	1.061	1.680	1.416
MUFA	0.348	----	3.506	2.399	2.935	2.478	2.701	2.560	2.297	3.518	2.802
PUFA	0.186	----	3.269	2.695	3.376	2.808	2.513	2.271	1.978	3.136	2.737
n-3	0.138	----	2.195	1.875	2.342	1.920	1.688	1.526	1.310	2.125	1.802
n-6	0.283	----	1.075	0.821	1.034	0.887	0.825	0.745	0.669	1.011	0.935
Somatic Tissue Polar Lipids											
			(6)	(6)	(7)	(6)	(6)	(7)	(7)	(8)	(6)
SFA	<0.001	----	0.543	0.511	0.550	0.654	0.680	0.641	0.590	0.542	0.521
MUFA	<0.001	----	0.283	0.251	0.294	0.355	0.458	0.431	0.334	0.297	0.257
PUFA	<0.001	----	1.045	1.024	1.124	1.389	1.508	1.502	1.349	1.124	1.025
n-3	<0.001	----	0.815	0.809	0.890	1.091	1.172	1.167	1.052	0.881	0.795
n-6	<0.001	----	0.230	0.215	0.234	0.297	0.337	0.336	0.297	0.242	0.230
Somatic Tissue Total Lipids											
			(5)	(6)	(7)	(4)	(6)	(7)	(7)	(7)	(6)
SFA	0.442	----	2.417	1.914	2.171	2.001	2.025	1.833	1.650	2.225	1.937
MUFA	0.568	----	3.427	2.650	3.229	2.820	3.159	2.991	2.630	3.810	3.059
PUFA	0.570	----	4.1013	3.720	4.500	4.160	4.022	3.773	3.328	4.266	3.762
n-3	0.466	----	2.856	2.684	3.232	2.991	2.860	2.693	2.362	3.012	2.597
n-6	0.682	----	1.246	1.036	1.268	1.169	1.162	1.080	0.966	1.254	1.165

Table III-8 cont... Seasonal changes in the content (g / kg carcass weight) of major fatty acid groups in various lipid compartments of female northern pike. Standard errors for these data are given in Appendix 10. Other details as in Table III-1.

		1987					1988					
Fatty Acid	p Value	May	June	July	August	Sept.	Jan.	March	May^{a}	May^{b}	June	Aug.
						Ovary Neutral Lipids						
			(6)	(6)	(7)	(7)	(7)	(7)	(2)	(4)	(8)	
SFA	<0.001	----	0.001	0.002	0.007	0.041	0.209	0.329	0.324	0.003	0.002	---
MUFA	<0.001	----	0.002	0.003	0.011	0.080	0.627	0.970	0.912	0.006	0.002	---
PUFA	<0.001	----	0.002	0.003	0.017	0.087	0.366	0.582	0.597	0.006	0.003	---
n-3	<0.001	----	0.002	0.002	0.013	0.061	0.240	0.387	0.395	0.004	0.002	---
n-6	<0.001	----	0.001	0.001	0.004	0.027	0.125	0.195	0.203	0.002	0.001	---
						Ovary Polar Lipids						
		(4)	(7)	(6)	(7)	(7)	(7)	(7)	(2)	(4)	(8)	
SFA	<0.001	0.016	0.007	0.011	0.029	0.141	0.790	1.173	1.089	0.017	0.008	---
MUFA	<0.001	0.012	0.005	0.008	0.021	0.103	0.738	1.084	0.973	0.014	0.005	---
PUFA	<0.001	0.024	0.010	0.014	0.042	0.233	1.443	2.170	2.013	0.027	0.011	---
n-3	<0.001	0.014	0.006	0.009	0.029	0.168	1.073	1.633	1.529	0.017	0.007	---
n-6	<0.001	0.010	0.004	0.005	0.013	0.065	0.371	0.537	0.484	0.010	0.004	---
					All Tissues Combined - Neutral Lipids							
			(6)	(6)	(7)	(4)	(6)	(7)	(2)	(4)	(7)	
SFA	0.315	----	2.139	1.405	1.628	1.404	1.540	1.521	1.002	1.122	1.682	---
MUFA	0.343	----	3.508	2.401	2.946	2.538	3.290	3.529	2.374	2.400	3.520	---
PUFA	0.571	----	3.272	2.699	3.392	2.881	2.862	2.853	1.861	2.049	3.138	---
n-3	0.520	----	2.196	1.877	2.355	1.972	1.920	1.913	1.219	1.364	2.127	---
n-6	0.623	----	1.075	0.822	1.038	0.909	0.943	0.940	0.642	0.685	1.011	---
					All Tissues Combined - Polar Lipids							
			(6)	(6)	(7)	(6)	(6)	(7)	(2)	(4)	(8)	
SFA	<0.001	----	0.550	0.522	0.579	0.806	1.422	1.814	1.667	0.612	0.550	---
MUFA	<0.001	----	0.288	0.259	0.315	0.466	1.159	1.515	1.287	0.353	0.303	---
PUFA	<0.001	----	1.055	1.039	1.167	1.639	2.868	3.672	3.380	1.349	1.134	---
n-3	<0.001	----	0.821	0.818	0.919	1.272	2.182	2.800	2.583	1.051	0.888	---
n-6	<0.001	----	0.234	0.220	0.247	0.367	0.686	0.873	0.797	0.298	0.246	---
					All Tissues Combined - Total Lipids							
			(5)	(6)	(7)	(4)	(6)	(7)	(2)	(4)	(7)	
SFA	0.002	----	2.426	1.927	2.207	2.145	2.962	3.335	2.669	1.734	2.234	---
MUFA	0.008	----	3.434	2.660	3.261	2.963	4.449	5.045	3.661	2.753	3.818	---
PUFA	<0.001	----	4.114	3.737	4.559	4.422	5.730	6.525	5.240	3.397	4.279	---
n-3	<0.001	----	2.863	2.695	3.274	3.178	4.101	4.713	3.802	2.414	3.020	---
n-6	0.003	----	1.250	1.042	1.285	1.244	1.629	1.812	1.439	0.983	1.259	---

a - data for pike which still contained mature eggs b - data for pike which had spawned all their eggs

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Chapter IV

A 'natural experiment' to determine the effect of ovarian recrudescence on the fatty acid composition of northern pike (_Esox lucius_ L.).

Introduction

Female northern pike undergo seasonal changes in fatty acid composition which are thought to be related to cycles of reproduction, dietary intake, and temperature (chapter III). However, the relative influence of these factors on tissue fatty acid composition of wild fish has not been clearly defined.

Populations of fish in the arctic provide an ideal 'natural experiment' with which to separate the physiological effects of ovarian recrudescence from those of other factors such as diet and temperature. Many fish species in the arctic appear to spawn only once every two or three years, apparently because they are unable to obtain or assimilate sufficient quantities of nutrients to grow mature ovaries each year (Miller and Kennedy 1948; Kennedy 1953,1954; Geen et al. 1966). Thus, at any given time such populations contain individual fish which are undergoing active ovarian recrudescence in preparation for the next spawning season and individuals whose ovaries remain in a pre-vitellogenic state for at least one spawning cycle.

The influence of ovarian maturation on fatty acid composition and metabolism is particularly large in the liver because this organ must incorporate the large amounts of lipid and other nutrients into vitellogenin, a plasma lipoprotein which is the major precursor of oocyte yolk (van Bohemen et al. 1981,1982; Ng and Idler 1983; Ng et al. 1984; Sheridan et al. 1985; Mommsen and Walsh 1988).

Ovarian recrudescence may also influence lipid and fatty acid metabolism in non-hepatic tissues. For example, if lipids required for ovarian growth cannot be obtained in sufficient quantities from the diet, many fish appear to transfer lipids from reserves in muscle or adipose tissue to the growing ovary (Wood 1958; Newsome and Leduc 1975; Nelson and McPherson 1986; Henderson and Almatar 1989; Jansen and Mackay 1989; Tanasichuk and Mackay 1989). Evidence suggests that certain fatty acids may be preferentially transferred from somatic to ovarian tissues (Henderson et al. 1984; Takama et al. 1985; Henderson and Almatar 1989). Even in those fish that do not deplete somatic lipid reserves during ovarian recrudescence, the large amounts of n-3 and n-6 essential fatty acids (EFAs) required by the ovary may reduce the quantities of dietary EFAs which are available for incorporation into somatic tissues and thereby alter their fatty acid composition.

The present chapter reports a comparison of fatty acid composition between female pike which either were or were not undergoing ovarian recrudescence in Campbell Lake, Northwest Territories. This comparison will indicate the role of ovarian recrudescence on tissue fatty acid composition while minimizing the seasonal effects of diet and temperature.

Materials and Methods

Adult female northern pike were collected from Campbell Lake (68° 12′N, 133° 25′E), N.W.T., using gill nets on three occasions from September 2 to 5′ 1988. Gill nets were set overnight and the catch was immediately transported to the Science Laboratory in Inuvik for further processing. Water temperature in Campbell Lake at the time of fish capture was 5 to 6 °C. In Inuvik, female pike were classified as either actively undergoing ovarian recrudescence or not undergoing ovarian recrudescence. Henceforth, these pike are referred to as recrudescing and non-recrudescing pike respectively. Criteria for designating pike as non-recrudescing were ovaries having a relatively translucent appearance and weighing between 0.3 and 0.7 % of total body weight. These features characterize pike ovaries which have not begun to recrudesce. Pike designated as recrudescing possessed ovaries which weighed more than 1.5 % of body weight and had the opaque, grainy appearance associated with the early stages of follicular development.

Five recrudescing and six non-recrudescing pike were selected for analysis; the selections were made so as to minimize differences in body weight between the two groups. Nevertheless, average body weight and standard length of the non-recrudescing fish (936 ± 265 g, 48.4 ± 5.0 cm) (mean ± SD) were significantly ($p<0.05$) smaller than those of the recrudescing fish (1447 ± 314 g, 54.7 ± 4.8 cm)(mean ± SD).

Although the exact size at which pike in the Inuvik area become sexually mature and capable of developing eggs is unknown, the smallest female pike we captured which was developing eggs weighed only 434 g and had a standard length of 38.2 cm. Since the smallest pike selected for fatty acid analysis weighed 654 g and measured 42.3 cm in standard length it is likely that all the non-recrudescing fish used in this study were sexually mature and capable of developing eggs and were not immature fish.

Tissues sampled for fatty acid analysis were ovary, liver, adipopancreatic (AP) tissue, and white muscle. Samples of these tissues were excised from each selected pike within 2 to 3 hours after their removal from the gill nets. Tissue samples were kept frozen in dry ice until the following day when lipid extraction was done by homogenizing exactly 2 g of frozen tissue in 40 ml of 2:1 chloroform/methanol (Folch et al. 1957) which contained BHT at approximately 0.1 % of total lipid concentration (Johnson 1971). Lipid extracts were filtered through Watman # 1 filter paper, bubbled with nitrogen, and stored in completely filled glass vials which were packed in dry ice until they had been transported back to Edmonton. Removal of non-lipids from chloroform/methanol extracts, separation of neutral and polar lipids, and fatty acid analysis were done in Edmonton as described in chapter III.

Differences between recrudescing and non-recrudescing pike were assessed using a t-test for unbalanced designs and are considered significant at $p<0.01$.

Results

Organ weights and total fatty acid content

A comparison of organ weights and fatty acid content between pike from Campbell Lake and those from Lac Ste. Anne is given in Table IV-1. These comparisons help in assessing whether conclusions about the influence of ovarian recrudescence on tissue fatty acid composition drawn from arctic pike also apply to better studied pike populations in Alberta. Data for the Lac Ste. Anne pike are given for two dates, July and September, at which these fish had ovary weights similar to those of the non-recrudescing and recrudescing pike from Campbell Lake. Ovaries of recrudescing Campbell Lake pike contained proportions of polar lipid fatty acids (PLFAs) and neutral lipid fatty acids (NLFAs) (70 % PLFAs and 30 % NLFAs by weight) identical to those found in recrudescing ovaries of Lac Ste. Anne pike (Table IV-1). Allowing for the lower ovary weight and earlier sampling of recrudescing pike from Campbell Lake (Sept. 2-5) than from Lac Ste. Anne (Sept. 22-24), it as apparent that increases in the concentration and content of NLFAs and PLFAs in ovaries during the early stages of ovarian recrudescence in Campbell Lake pike are of approximately similar magnitude to those of Lac Ste. Anne pike (Table IV-1). Differences in average liver weight between recrudescing and non-recrudescing pike from Campbell Lake were not significant but did resemble the increase in liver weight which occurs between July and September in Lac Ste. Anne pike (Table IV-1). Recrudescing and non-recrudescing pike from Campbell Lake did not differ significantly in their weight of AP tissue, but the non-recrudescing pike had only about half as much AP tissue (3.5 g/kg carcass wt) as pike from Lac Ste. Anne (6.4 to 8 g/kg carcass wt; Table IV-1 and Fig. II-1).

Concentrations and total amounts of NLFAs in liver, muscle, and AP tissue did not differ significantly between recrudescing and non-recrudescing pike from Campbell Lake. However, both groups of Campbell Lake pike had much smaller total somatic NLFA reserves (0.7 g/kg carcass wt in non-recrudescing pike and 2.9 g/kg carcass wt in recrudescing pike; Table IV-1) compared to pike in Lac Ste. Anne (5.3 to 8.9 g/kg carcass wt; Fig. II-4).

There were no significant differences between recrudescing and non-recrudescing pike from Campbell Lake in the PLFA concentrations of the three somatic tissues or the PLFA content of muscle and AP tissue (Table IV-1). The recrudescing pike did possess greater total quantities of PLFAs in their liver compared to non-recrudescing pike, and this trend accompanied ovarian recrudescence in Lac Ste. Anne pike as well (Table IV-1; Fig. II-3). It is also worth noting that concentrations of PLFAs in muscle of Campbell Lake pike were somewhat lower than those found in Lac Ste. Anne pike in September (Table IV-1).

Fatty acid compositions

Recrudescing and non-recrudescing Campbell Lake pike differed significantly in tissue fatty acid composition. Ovarian recrudescence in Campbell Lake pike involved significant declines in the percentage of SFAs and increases in the percentage of MUFAs in ovarian NLs (Fig. IV-1). Liver NLs of recrudescing pike contained percentages of MUFAs that were 11 wt % higher and percentages of n-3 fatty acids 13 wt % lower than in liver NLs of non-recrudescing pike (Fig. IV-1). Percentages of the major fatty acid groups in NLs of muscle and AP tissue did not differ significantly between recrudescing and non-recrudescing pike (Fig. IV-1).

Ovarian PLs contained significantly lower percentages of MUFAs and higher percentages of n-3 fatty acids in recrudescing than in non-recrudescing pike (Fig. IV-2). Recrudescing pike contained significantly lower percentages of total PUFAs and n-3 fatty acids and higher percentages of n-6 fatty acids in their liver PLs compared to non-recrudescing pike (Fig. IV-2). The largest differences in PLFA composition between the two groups of Campbell Lake pike occurred in muscle; percentages of n-3 fatty acids were 6 wt % lower and percentages of n-6 fatty acids were 4 wt % higher in recrudescing than in non-recrudescing pike (Fig. IV-2). Differences between recrudescing and non-recrudescing pike in the fatty acid composition of AP tissue PLs were not statistically significant but were qualitatively similar to the differences in PLFA composition of muscle (Fig. IV-2).

Percentages of 16:0 in ovarian NLs were significantly lower in recrudescing than in non-recrudescing pike (Table IV-2). Among individual fatty acids in ovarian NLs, 18:1n9 showed the greatest differences in percent composition between the two pike groups and largely accounted for the higher percentage of MUFAs in NLs of recrudescing ovaries than non-recrudescing ones (Table IV-2). Although recrudescing pike contained higher percentages of 18:2n6 and 18:3n3 in their ovarian NLs compared to non-recrudescing pike, they had lower percentages of 20:4n6, 22:5n6, and 20:5n3 (Table IV-2), so that the total percentages of n-3 and n-6 fatty acids did not differ significantly between the two pike groups (Fig. IV-1).

Differences between recrudescing and non-recrudescing pike in the percentages of MUFAs and n-3 fatty acids in liver NLs (Fig. IV-1) were due largely to higher proportions of 18:1n9 and lower percentages of 22:6n3 in the recrudescing pike (Table IV-2). Other fatty acids whose percent composition in liver NLs differed significantly between the two pike groups were 16:1n7, 18:2n6, and 18:3n3 which represented higher percentages in recrudescing pike, and 22:5n6 and 22:5n3 which were present in lower percentages in recrudescing than in non-recrudescing pike (Table IV-2). There were no significant differences between recrudescing and non-recrudescing pike in the percent composition of individual fatty acids in NLs of muscle and AP tissue (Table IV-2).

Although the total percentage of SFAs in ovarian and liver PLs did not differ between recrudescing and non-recrudescing pike (Fig. IV-2), the recrudescing fish had significantly higher percentages of 16:0 in PLs of both liver and ovary which were offset by lower percentages of 14:0 and 18:0 (Table IV-3). Ovarian recrudescence resulted in increased percentages of 18:2n6 on PLs of ovary and liver, and increased percentages of 20:4n6 in liver PLs (Table IV-3). Percentages of 20:5n3 in liver PLs were significantly lower in recrudescing than in non-recrudescing pike. The recrudescing pike possessed a significantly higher percentage of 22:6n3 in ovarian PLs (Table IV-3), which meant that the percentage of total n-3 fatty acids in ovarian PLs was also significantly higher than in non-recrudescing pike (Fig. IV-2).

Differences between the two pike groups in the percentages of n-3 and n-6 fatty acids in muscle PLs (Fig. IV-2) were due primarily to higher levels of 20:4n6 and lower percentages of 22:6n3 in the recrudescing pike (Table IV-3). Percentages of 18:2n6 showed smaller but significant differences between the two pike groups. In PLs of AP tissue, percentages of 18:2n6 were higher and those of 22:6n3 lower in recrudescing than in non-recrudescing pike (Table IV-3), but these and other differences in fatty acid composition were not significant at the $p < 0.01$ level (Table IV-3).

Because the recrudescing and non-recrudescing pike differed in average body weight, the possibility of correlations between body weight and the physiological variables measured was examined. None of the fatty acid classes whose percent composition differed between the two pike groups exhibited a consistent correlation with body weight. For example, the percentage of n-3 fatty acids in muscle PLs appeared to decrease with increasing body weight in the non-recrudescing pike, but appeared to follow the opposite trend in the recrudescing pike. Furthermore, when individual fish of similar body weight are compared, differences in the percentage of n-3 fatty acids between recrudescing and non-recrudescing fish are still apparent. On this basis, differences in tissue fatty acid composition between recrudescing and non-recrudescing pike are judged to be due primarily to reproductive status and not body size.

Discussion

Differences in fatty acid content and percent composition between recrudescing and non-recrudescing pike in Campbell Lake should help in determining which of the seasonal changes observed in the somatic tissues of Lac Ste. Anne pike (chapters II and III) may be related to ovarian recrudescence. This assumes that the weight and fatty acid content and composition of pike tissues, and the effects of ovarian recrudescence on these parameters, are similar in Campbell Lake and Lac Ste. Anne.

For the most part, the wet weight, total NLFA and PLFA content, and fatty acid composition of tissues from recrudescing Campbell Lake pike were very similar to those of pike in Lac Ste. Anne in September (compare Tables IV-1,2,3, with Figs. III-4 to 15). The only exceptions to this are the total quantities of NLFAs in muscle and AP tissue (Table IV-1) and the fatty acid composition of muscle NLs. Reasons for these differences between Campbell Lake and Lac Ste. Anne pike will be discussed later.

Pike in Campbell Lake and those in Lac Ste. Anne exhibited very similar changes in the weight and fatty acid content and composition of the ovaries during the early part of recrudescence which suggests that these changes may be characteristic of pike as a species. Table IV-1 shows that increases in the weight and NLFA and PLFA content of pike ovaries during late August and early September are of similar magnitude in the two lakes when allowances are made for the earlier sampling of pike from Campbell Lake than from Lac Ste. Anne. Additionally, the ratios of PLFAs to NLFAs (70 % PLFAs : 30 % NLFAs) in the recrudescing ovaries are also very similar in Campbell Lake and Lac Ste. Anne pike (Table IV-1; Fig. II-2a,b). In both populations, the early part of ovarian recrudescence involved decreases in the percentage of SFAs and increases in the percentage of MUFAs in ovary NLs, while in ovary PLs the percentage of MUFAs decreased and n-3 PUFAs increased (compare Figs. IV-1,2 and Figs. III-4,6). The ovaries of Campbell Lake pike even exhibited the same reciprocal changes in 18:2n6 and 18:3n3 versus long chain PUFAs in NLs, and in 18:2n6 versus long chain n-6 PUFAs in PLs, which occurred in Lac Ste. Anne pike (Tables IV-2,3).

A few changes in ovary fatty acid composition observed in Lac Ste. Anne pike from July to September, namely changes in n-3 PUFAs in NLs and decreases in SFAs and n-6 PUFAs in PLs (Figs. III-4,6) were not observed in Campbell Lake pike (Figs. IV-1,2). It is not known whether this reflects real differences in ovary fatty acid composition between geographic locations or merely indicates that the Campbell Lake fish were sampled too early, before such differences in fatty acid composition could develop.

Overall, a high degree of similarity exists between Campbell Lake and Lac Ste. Anne pike in the fatty acid content and composition of somatic tissues and in changes in these parameters in the ovaries during recrudescence. This suggests that conclusions drawn from Campbell Lake pike about the influence of ovarian recrudescence on the fatty acid composition of somatic tissues may also apply to pike in Lac Ste. Anne.

Ovarian recrudescence in pike in Campbell Lake involved increases in liver weight and in liver PLFA concentration and content, although only the increase in liver PLFA content was statistically significant (Table IV-1). This suggests that significant increases in liver weight and in liver PLFA concentration and content which occur in Lac Ste. Anne pike from July to September (Figs. II-1,2,3) are at least partly associated with ovarian recrudescence.

Recrudescing Campbell Lake pike did not have lower liver NLFA concentrations or contents compared to non-recrudescing pike (Table IV-1). Therefore, the large decline in liver NLFA content which was observed in Lac Ste. Anne pike throughout the summer and winter of 1987 was probably not associated with ovarian recrudescence, but perhaps with other factors such as changes in the rate of food intake.

Increases in the percentage of MUFAs, decreases in the percentage of total n-3 fatty acids, and reciprocal changes in 18:2n6 and 18:3n3 versus long chain PUFAs in liver NLs of Lac Ste. Anne pike during late summer and early winter (Figs. III-4,9) were probably due to ovarian recrudescence because changes of similar direction and magnitude were observed in Campbell Lake pike (Fig. IV-1; Table IV-2). Data obtained from Campbell Lake pike also indicate that decreases in the percentage of n-3 PUFAs in liver PLs of pike in Lac Ste. Anne during early winter (Fig. III-6) are probably due to ovarian recrudescence (Fig. IV-2). These changes in the fatty acid composition of liver NLs and PLs may reflect the synthesis of vitellogenin in liver in response to estrogen hormones released from the recrudescing ovary (van Bohemen et al. 1982; Ng et al. 1984; Mommsen and Walsh 1988).

Decreases in the percentage of SFAs and increases in MUFAs in liver PLs occurred during late summer in Lac Ste. Anne pike (Fig. III-6), but were not associated with ovarian recrudescence in Campbell Lake pike (Fig. IV-2). Perhaps these changes serve primarily to increase the unsaturation of liver PLs during cold acclimation and are not directly attributable to ovarian recrudescence.

Female pike in Lac Ste. Anne exhibited highly significant decreases in the percentage of n-3 PUFAs and increases in MUFAs in NLs of muscle and AP tissue between September and January (Fig. III-5). It was hypothesized that this may reflect adaptations to divert dietary n-3 PUFAs away from somatic NLs and thereby conserve these EFAs for use in ovary growth and temperature induced membrane PL restructuring. Ovarian recrudescence in Campbell Lake pike also appeared to involve decreases in the amount of n-3 PUFAs and increases in MUFAs in muscle and AP tissue NLs although these changes were not statistically significant (Fig. IV-1). However, that such changes occurred in NLs of both muscle and AP tissue of Campbell Lake pike suggests that they may be real responses to ovarian recrudescence and provides some support for the above hypothesis.

Ovarian recrudescence in Campbell Lake pike appears to significantly reduce the percentage of n-3 fatty acids and increase the percentage of n-6 PUFAs in muscle PLs of pike (Fig. IV-2). However, pike undergoing ovarian recrudescence from August to March in Lac Ste. Anne experience significant increases in the percentage of n-3 PUFAs in muscle and AP tissue PLs, with no change in the percentage of n-6 PUFAs (Fig. III-7). It is difficult to explain why ovarian recrudescence should be associated with reduced percentages of n-3 PUFAs and elevated percentages of n-6 PUFAs in muscle PLs of pike in Campbell Lake but not in Lac Ste. Anne. The only studies which contain information on the relationship between body size and the fatty acid composition of fish muscle have examined only total lipids and yielded conflicting results (Jangaard et al. 1967; Tidwell and Robinete 1990).

The explanation for differences in muscle PL fatty acid composition between recrudescing and non-recrudescing pike in Campbell Lake may lie in the previous history of these fish. The pike designated as non-recrudescing in September were probably undergoing ovarian growth during the previous winter. If Campbell Lake pike catabolize somatic tissues during the last stages of ovarian recrudescence (ie: after March) as do pike in Lac Ste. Anne, then higher percentages of n-3 PUFAs in muscle PLs of non-recrudescing Campbell lake pike may reflect the effects of starvation. Laboratory studies have shown that starvation in fish may actually increase percentages of n-3 PUFAs in tissue PLs, apparently because n-3 PUFAs are preferentially conserved as the total PL pool decreases in size (Casteldine and Buckley 1980; Jezierska et al. 1982).

Both recrudescing and non-recrudescing pike in Campbell Lake had much lower reserves of NL in their muscle and AP tissue compared to Lac Ste. Anne pike (Table IV-1). This supports the suspicion that the slow growth rate and 2 or 3 year spawning cycles of fish in extreme northern latitudes result from energy or nutrient limitations due to lower average temperatures, shorter growing seasons, and perhaps lower food availability (Mackay 1989).

Campbell Lake pike exhibited higher percentages of SFAs and lower percentages of MUFAs in muscle NLs compared to pike from Lac Ste. Anne. These differences may be related to diet or to the large differences in total NLFA content of muscle between the two pike populations. Percentages of n-3 PUFAs in muscle PLs were also somewhat lower in recrudescing Campbell Lake pike (41.4 %) than in Lac Ste. Anne pike in September (44.9 % - Fig. III-7) but are not low enough to indicate significant deficiencies of n-3 fatty acids in arctic pike (Castell et al. 1972; Yu et al. 1977).

From August to March, a 1 kg carcass weight pike in Lac Ste. Anne accumulates in its ovaries a total of about 6.3 g of fatty acids, of which 2.7 g are n-3 and n-6 PUFAs (Fig. II-3 and Table III-8). If such large quantities of fatty acids also accumulate in the ovaries of Campbell Lake pike, then quantities of total fatty acids (2.9 g/kg carcass wt) and PUFAs (1.0 g/kg carcass wt) in the NLs of the three somatic tissues of these fish (calculated from Table IV-1 and Fig. IV-1) would be totally inadequate to meet the needs of ovarian recrudescence. It is highly likely that pike in Campbell Lake, like those in Lac Ste. Anne, must rely largely on food eaten over winter to supply the nutrients required for ovarian recrudescence.

Table IV-1. Organ weights and fatty acid content of female pike from Campbell Lake, N.W.T., and Lac Ste. Anne, Alberta. Data are given as means ± S.E., with n values in parentheses.

	Campbell Lake, Sept. 2-5			Lac Ste. Anne	
	p value[c]	non-recrudescing	recrudescing	July 27-29	September 22-24
ovary wt[a]	< 0.001	5.2 ± 0.6 (6)	22.7 ± 2.9 (5)	4.9 ± 0.6 (6)	29.0 ± 3.6 (7)
liver wt	0.162	12.4 ± 1.3 (6)	15.4 ± 1.6 (5)	12.1 ± 0.8 (6)	16.8 ± 1.0 (7)
AP tissue wt	0.052	3.5 ± 0.3 (6)	6.7 ± 1.6 (5)	6.8 ± 0.9 (6)	6.4 ± 0.3 (7)
ovary:					
NLFA conc.[b]	< 0.001	0.10 ± 0.02 (6)	0.58 ± 0.07 (5)	0.17 ± 0.02 (6)	0.70 ± 0.07 (7)
NLFA content[a]	0.005	0.006 ± 0.001 (6)	0.14 ± 0.04 (5)	0.008 ± 0.002 (6)	0.21 ± 0.05 (7)
liver:					
NLFA conc.	0.281	1.37 ± 0.10 (6)	2.17 ± 0.76 (5)	5.0 ± 1.0 (6)	2.5 ± 0.6 (5)
NLFA content	0.179	0.17 ± 0.02 (6)	0.35 ± 0.13 (5)	0.59 ± 0.11 (6)	0.39 ± 0.12 (5)
muscle:					
NLFA conc.	0.702	0.04 ± 0.004 (6)	0.04 ± 0.01 (5)	0.41 ± 0.08 (6)	0.73 ± 0.22 (6)
NLFA content	0.702	0.24 ± 0.02 (6)	0.22 ± 0.05 (5)	2.23 ± 0.44 (6)	4.02 ± 1.20 (6)
AP tissue:					
NLFA conc.	0.089	7.4 ± 2.3 (6)	26.0 ± 10.4 (5)	56.9 ± 7.2 (6)	52.9 ± 2.7 (7)
NLFA content	0.110	0.29 ± 0.11 (6)	2.35 ± 1.28 (5)	4.2 ± 0.9 (6)	3.4 ± 0.3 (7)
ovary:					
PLFA conc.	< 0.001	0.72 ± 0.04 (6)	1.33 ± 0.09 (5)	0.69 ± 0.03 (6)	1.62 ± 0.13 (7)
PLFA content	0.002	0.038 ± 0.006 (6)	0.31 ± 0.06 (5)	0.034 ± 0.005 (6)	0.49 ± 0.11 (7)
liver:					
PLFA conc.	0.046	1.46 ± 0.08 (6)	1.71 ± 0.07 (5)	1.20 ± 0.09 (6)	1.69 ± 0.05 (7)
PLFA content	0.009	0.18 ± 0.02 (6)	0.26 ± 0.02 (5)	0.14 ± 0.01 (6)	0.28 ± 0.02 (7)
muscle:					
PLFA conc.	0.346	0.28 ± 0.01 (6)	0.30 ± 0.02 (5)	0.31 ± 0.01 (6)	0.39 ± 0.01 (6)
PLFA content	0.346	1.53 ± 0.08 (6)	1.65 ± 0.10 (5)	1.70 ± 0.07 (6)	2.17 ± 0.07 (6)
AP tissue:					
PLFA conc.	0.329	0.94 ± 0.05 (6)	0.80 ± 0.13 (5)	0.47 ± 0.10 (6)	0.58 ± 0.05 (7)
PLFA content	0.121	0.033 ± 0.004 (6)	0.047 ± 0.008 (5)	0.027 ± 0.002 (6)	0.037 ± 0.004 (7)

a - the weight and fatty acid content of organs and tissues are expressed as grams / kg carcass wt.

b - fatty acid concentrations are expressed as % of tissue wet wt.

c - results of t-test (for unbalanced designs) for significance of differences between recrudescing and non-recrudescing pike

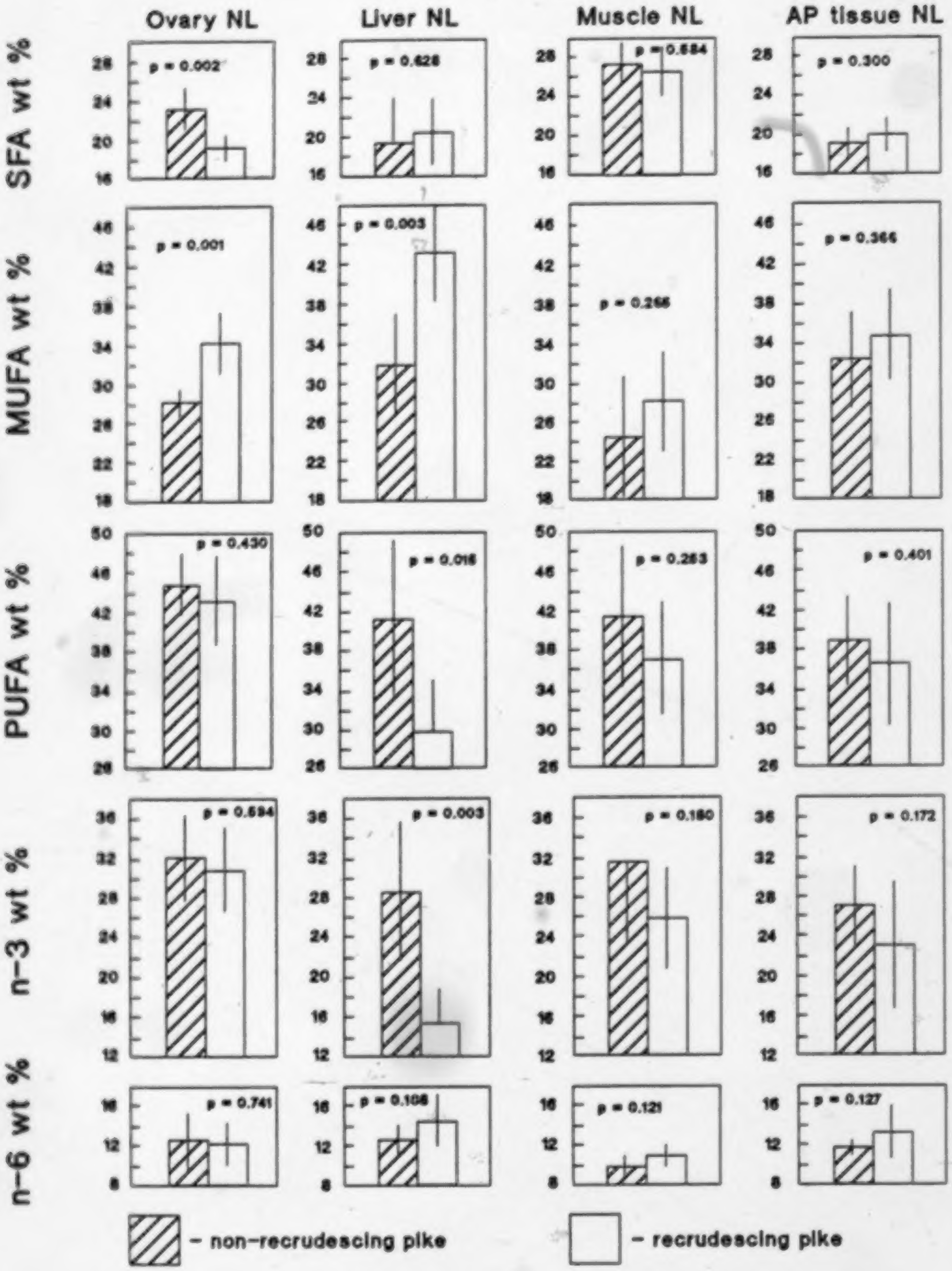

Figure IV-1. Percentages of major fatty acid groups in tissue neutral lipids (NL) of recrudescing and non-recrudescing female pike from Campbell Lake. Means and 95 % C.I.'s are shown. n values are given in Table IV-2. P values refer to the significance of differences between recrudescing and non-recrudescing pike (t-test for unbalanced designs).

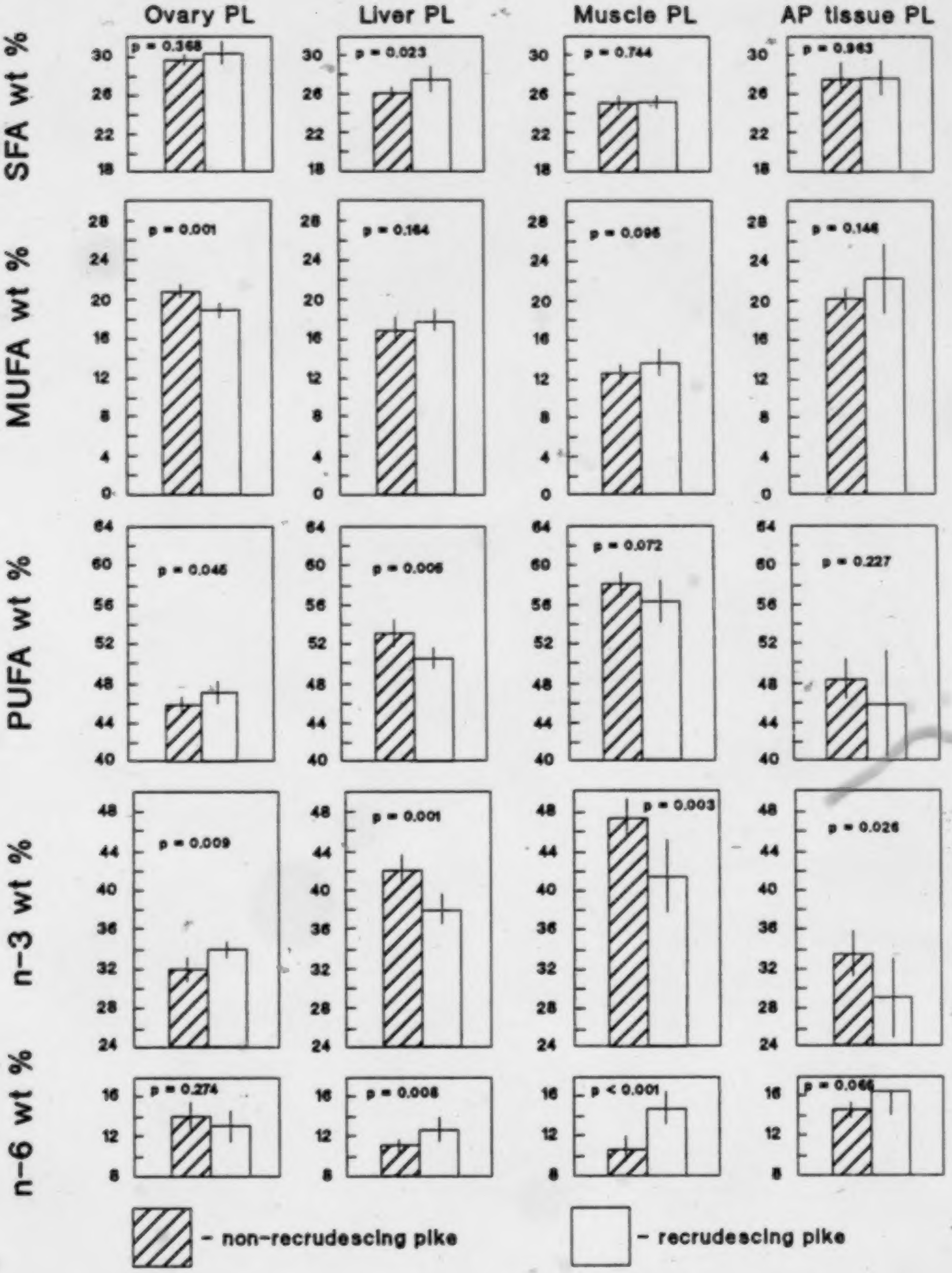

Figure IV-2. Percentages of major fatty acid groups in tissue polar lipids (PL) of recrudescing and non-recrudescing female pike from Campbell Lake. Means and 95 % C.I.'s are shown. n values are given in Table IV-3. P values refer to the significance of differences between recrudescing and non-recrudescing pike (t-test for unbalanced designs).

Table IV-2. Neutral lipid fatty acid compositions of tissues from recrudescing and non-recrudescing female pike from Campbell Lake. Data are given as mean ± SE.

Fatty Acid	Ovary				Liver			
	p value[c]	$\|A-B\|^b$	Non-recrud. (A) (n=6)	Recrud. (B) (n=5)	p value[c]	$\|C-D\|^b$	Non-recrud. (C) (n=6)	Recrud. (D) (n=5)
16:0	0.001	2.7	17.2 ± 0.36[a]	14.5 ± 0.41	0.195	2.0	12.3 ± 1.04	14.3 ± 0.92
18:0	0.026	1.4	6.0 ± 0.47	4.6 ± 0.18	0.366	0.8	7.1 ± 0.78	6.3 ± 0.33
16:1n7	0.668	0.3	10.9 ± 0.66	11.2 ± 0.25	0.003	2.4	9.9 ± 0.40	12.3 ± 0.40
18:1n9	0.001	5.7	17.3 ± 0.40	23.0 ± 1.06	0.004	9.0	22.0 ± 1.74	31.0 ± 1.53
18:2n6	0.003	2.4	3.6 ± 0.36	6.0 ± 0.45	0.003	3.3	6.8 ± 0.45	10.1 ± 0.73
20:4n6	0.043	2.0	6.9 ± 0.73	4.9 ± 0.34	0.644	0.2	4.0 ± 0.36	3.8 ± 0.24
22:5n6	0.066	0.8	2.2 ± 0.41	1.4 ± 0.04	<0.001	1.3	2.0 ± 0.19	0.7 ± 0.09
18:3n3	0.003	1.6	1.8 ± 0.28	3.4 ± 0.27	<0.001	1.9	3.5 ± 0.24	5.4 ± 0.25
20:5n3	0.021	2.4	8.2 ± 0.64	5.8 ± 0.53	0.069	2.8	6.8 ± 1.18	4.0 ± 0.37
22:5n3	0.850	0.0	2.1 ± 0.12	2.1 ± 0.16	<0.001	2.3	3.4 ± 0.29	1.1 ± 0.16
22:6n3	0.812	0.5	20.0 ± 1.23	19.5 ± 1.53	0.001	10.0	14.8 ± 1.71	4.8 ± 1.18
others	0.436	0.3	3.9 ± 0.26	3.6 ± 0.23	0.130	1.2	7.3 ± 0.62	6.1 ± 0.03
SFA	0.002	4.0	23.1 ± 0.77	19.1 ± 0.48	0.628	1.1	19.5 ± 1.77	20.6 ± 1.22
MUFA	0.001	6.0	28.2 ± 0.54	34.2 ± 1.14	0.003	11.4	31.9 ± 2.03	43.3 ± 1.85
PUFA	0.430	1.7	44.8 ± 1.13	43.1 ± 1.65	0.015	11.3	41.3 ± 3.05	30.0 ± 1.90
all n-6	0.741	0.4	12.7 ± 1.00	12.3 ± 0.78	0.108	1.8	12.8 ± 0.53	14.6 ± 0.94
all n-3	0.594	1.3	32.1 ± 1.57	30.8 ± 1.56	0.003	13.1	28.5 ± 2.74	15.4 ± 1.25

a - fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in tissue NL's

b - indicates the absolute value of the difference in the indicated variable between recrudescing and non-recrudescing pike.

c - results of t-test (for unbalanced designs) for significance of differences between recrudescing and non-recrudescing pike

Table IV-2 continued... Neutral lipid fatty acid compositions of tissues from recrudescing and non-recrudescing female pike from Campbell Lake. Data are given as mean ± SE.

Fatty Acid	Muscle				Adipopancreatic Tissue			
	p value[c]	$\lvert A-B \rvert$[b]	Non-recrud. (A) (n=6)	Recrud. (B) (n=5)	p value[c]	$\lvert C-D \rvert$[b]	Non-recrud. (C) (n=6)	Recrud. (D) (n=5)
16:0	0.759	0.2	17.6 ± 0.51[a]	17.4 ± 0.37	0.531	0.4	14.0 ± 0.38	14.4 ± 0.40
18:0	0.558	0.5	9.8 ± 0.55	9.3 ± 0.62	0.292	0.6	5.2 ± 0.44	5.8 ± 0.24
16:1n7	0.732	0.5	8.5 ± 1.35	9.0 ± 0.76	0.118	1.0	11.9 ± 0.42	12.9 ± 0.37
18:1n9	0.107	3.2	16.0 ± 1.25	19.2 ± 1.28	0.534	1.5	20.4 ± 1.61	21.9 ± 1.64
18:2n6	0.105	1.0	3.9 ± 0.52	4.9 ± 0.19	0.171	1.3	6.5 ± 0.40	7.8 ± 0.80
20:4n6	0.399	0.3	4.5 ± 0.22	4.8 ± 0.21	0.032	0.9	3.2 ± 0.18	4.1 ± 0.31
22:5n6	0.428	0.2	1.6 ± 0.19	1.4 ± 0.17	0.262	0.6	2.1 ± 0.37	1.5 ± 0.33
18:3n3	0.038	1.4	2.9 ± 0.31	4.3 ± 0.50	0.741	0.2	6.8 ± 0.25	7.0 ± 0.40
20:5n3	0.076	1.9	7.3 ± 0.75	5.4 ± 0.41	0.394	0.5	4.6 ± 0.36	4.1 ± 0.43
22:5n3	0.284	0.2	1.7 ± 0.12	1.9 ± 0.25	0.949	0.0	2.5 ± 0.29	2.5 ± 0.53
22:6n3	0.120	5.4	19.6 ± 2.45	14.2 ± 1.80	0.233	3.7	13.2 ± 1.54	9.5 ± 2.49
others	0.423	1.3	6.7 ± 1.25	8.0 ± 0.80	0.194	1.0	9.6 ± 0.58	8.6 ± 0.32
SFA	0.584	0.7	27.4 ± 0.86	26.7 ± 0.92	0.300	0.9	19.2 ± 0.61	20.1 ± 0.61
MUFA	0.265	3.8	24.5 ± 2.47	28.3 ± 1.85	0.366	2.5	32.3 ± 1.91	34.8 ± 1.69
PUFA	0.253	4.4	41.4 ± 2.79	37.0 ± 2.08	0.401	2.4	38.9 ± 1.74	36.5 ± 2.24
all n-6	0.121	1.2	9.9 ± 0.49	11.1 ± 0.44	0.127	1.5	11.9 ± 0.32	13.4 ± 0.93
all n-3	0.180	5.6	31.5 ± 3.10	25.9 ± 1.87	0.172	4.0	27.1 ± 1.58	23.1 ± 2.26

a - fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in tissue NL's

b - indicates the absolute value of the difference in the indicated variable between recrudescing and non-recrudescing pike.

c - results of t-test (for unbalanced designs) for significance of differences between recrudescing and non-recrudescing pike

Table IV-3. Polar lipid fatty acid compositions of tissues from recrudescing and non-recrudescing female pike from Campbell Lake. Data are given as mean ± SE.

Fatty Acid	Ovary				Liver			
	p value[c]	|A-B|[b]	Non-recrud. (A) (n=6)	Recrud. (B) (n=5)	p value[c]	|C-D|[b]	Non-recrud. (C) (n=6)	Recrud.(D) (n=5)
14:0	0.004	0.5	1.4 ± 0.10[a]	0.9 ± 0.06	0.102	0.3	1.2 ± 0.07	0.9 ± 0.12
16:0	<0.001	3.4	20.0 ± 0.27	23.4 ± 0.57	<0.001	3.0	17.4 ± 0.29	20.4 ± 0.54
18:0	<0.001	2.5	8.5 ± 0.15	6.0 ± 0.18	<0.001	1.3	7.6 ± 0.10	6.3 ± 0.05
16:1n7	<0.001	1.1	7.0 ± 0.07	5.9 ± 0.16	0.816	0.1	5.3 ± 0.17	5.4 ± 0.31
18:1n9	0.061	0.8	13.8 ± 0.33	13.0 ± 0.14	0.088	1.0	11.5 ± 0.40	12.5 ± 0.22
18:2n6	<0.001	0.7	1.8 ± 0.08	2.5 ± 0.11	0.005	0.9	2.3 ± 0.10	3.2 ± 0.22
20:4n6	0.091	1.3	10.4 ± 0.47	9.1 ± 0.46	0.007	1.2	7.1 ± 0.17	8.3 ± 0.35
22:5n6	0.021	0.4	1.9 ± 0.12	1.5 ± 0.05	<0.001	0.4	1.7 ± 0.06	1.3 ± 0.03
18:3n3	0.318	0.2	1.4 ± 0.01	1.6 ± 0.11	0.834	0.1	2.3 ± 0.12	2.2 ± 0.16
20:5n3	0.034	1.7	8.6 ± 0.24	6.9 ± 0.64	<0.001	3.4	9.3 ± 0.33	5.9 ± 0.58
22:5n3	0.142	0.3	2.0 ± 0.08	2.3 ± 0.20	0.319	0.3	1.8 ± 0.11	2.1 ± 0.28
22:6n3	0.004	3.4	19.8 ± 0.31	23.2 ± 0.76	0.487	0.9	28.6 ± 0.59	27.7 ± 1.28
others	0.175	0.3	3.4 ± 0.13	3.7 ± 0.18	0.860	0.1	3.8 ± 0.25	3.9 ± 0.14
SFA	0.368	0.5	29.8 ± 0.16	30.3 ± 0.43	0.023	1.4	26.2 ± 0.24	27.6 ± 0.49
MUFA	0.001	1.9	20.8 ± 0.28	18.9 ± 0.28	0.164	1.1	16.8 ± 0.51	17.9 ± 0.41
PUFA	0.045	1.2	45.9 ± 0.26	47.1 ± 0.41	0.005	2.5	53.1 ± 0.51	50.6 ± 0.39
all n-6	0.274	0.9	14.1 ± 0.54	13.2 ± 0.57	0.008	1.6	11.2 ± 0.21	12.8 ± 0.46
all n-3	0.009	2.0	31.9 ± 0.50	33.9 ± 0.33	0.001	4.1	42.0 ± 0.62	37.9 ± 0.58

a - fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in tissue PL's

b - indicates the absolute value of the difference in the indicated variable between recrudescing and non-recrudescing pike.

c - results of t-test (for unbalanced designs) for significance of differences between recrudescing and non-recrudescing pike

Table IV-3. continued... Polar lipid fatty acid compositions of tissues from recrudescing and non-recrudescing female pike from Campbell Lake. Data are given as mean ± SE.

Fatty Acid	Muscle				Adipopancreatic Tissue			
	p value[c]	$\lvert A-B \rvert$[b]	Non-recrud. (A) (n=6)	Recrud. (B) (n=5)	p value[c]	$\lvert C-D \rvert$[b]	Non-recrud. (C) (n=6)	Recrud. (D) (n=5)
14:0	0.860	0.1	0.7 ± 0.02[a]	0.6 ± 0.03	0.344	0.3	1.5 ± 0.12	1.2 ± 0.22
16:0	0.170	0.5	18.0 ± 0.22	18.5 ± 0.31	0.663	0.2	17.7 ± 0.39	17.9 ± 0.40
18:0	0.018	0.4	6.4 ± 0.11	6.0 ± 0.08	0.819	0.1	8.7 ± 0.18	8.6 ± 0.14
16:1n7	0.040	0.3	2.8 ± 0.08	3.1 ± 0.14	0.128	0.7	6.0 ± 0.10	6.7 ± 0.46
18:1n9	0.138	0.8	9.6 ± 0.30	10.4 ± 0.38	0.167	1.3	14.1 ± 0.36	15.4 ± 0.89
18:2n6	<0.001	1.3	2.1 ± 0.11	3.4 ± 0.24	0.011	1.1	3.2 ± 0.21	4.3 ± 0.24
20:4n6	0.001	3.0	6.3 ± 0.39	9.3 ± 0.54	0.193	1.1	9.7 ± 0.31	10.8 ± 0.79
22:5n6	0.170	0.2	2.3 ± 0.11	2.1 ± 0.09	0.092	0.2	1.8 ± 0.11	1.6 ± 0.05
18:3n3	0.014	0.7	1.5 ± 0.11	2.2 ± 0.20	0.683	0.1	3.0 ± 0.16	3.1 ± 0.23
20:5n3	0.298	0.6	7.7 ± 0.15	8.3 ± 0.56	0.231	1.0	7.6 ± 0.40	6.6 ± 0.68
22:5n3	0.074	0.3	2.4 ± 0.09	2.7 ± 0.15	0.176	0.2	2.1 ± 0.08	2.3 ± 0.13
22:6n3	0.002	7.6	35.9 ± 0.91	28.3 ± 1.50	0.022	3.8	20.9 ± 0.61	17.1 ± 1.34
others	0.041	0.6	4.4 ± 0.16	5.0 ± 0.17	0.019	0.6	3.8 ± 0.10	4.4 ± 0.19
SFA	0.744	0.1	25.1 ± 0.28	25.2 ± 0.27	0.963	0.0	27.8 ± 0.59	27.8 ± 0.66
MUFA	0.095	1.1	12.4 ± 0.37	13.5 ± 0.51	0.146	2.1	20.0 ± 0.45	22.1 ± 1.34
PUFA	0.072	1.8	58.1 ± 0.48	56.3 ± 0.81	0.227	2.6	48.3 ± 0.76	45.7 ± 2.03
all n-6	<0.001	4.1	10.7 ± 0.49	14.8 ± 0.63	0.065	1.8	14.8 ± 0.29	16.6 ± 0.92
all n-3	0.003	6.0	47.4 ± 0.83	41.4 ± 1.34	0.026	4.4	33.5 ± 0.94	29.1 ± 1.46

a - fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in tissue PL's

b - indicates the absolute value of the difference in the indicated variable between recrudescing and non-recrudescing pike.

c - results of t-test (for unbalanced designs) for significance of differences between recrudescing and non-recrudescing pike

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Chapter V

How closely does the fatty acid composition of female northern pike (Esox lucius L.) resemble that of their diet ?

Introduction

The role of diet in the seasonal cycles of tissue fatty acid composition in northern pike (chapter III) is difficult to evaluate unless the fatty acid composition of the pike's diet is known. To date, the fatty acid compositions of the natural foods of wild fish have not been well characterized (Henderson and Tocher 1987; Sargent et al. 1989).

The available evidence suggests that in aquatic systems phytoplankton and other plants synthesize and accumulate n-3 and n-6 fatty acids, predominantly those with chain lengths of 16 or 18 carbon atoms (Sargent and Whittle 1981; Morris 1985; Fraser et al. 1989). Invertebrates such as zooplankton and aquatic insects appear to perform most of the chain elongation and further desaturation of these EFAs to 20:4n6 and 20:5n3 (Hanson et al. 1985). However, freshwater aquatic insects do not appear to accumulate significant quantities of 22:6n3 (Hanson 1985), which is the dominant n-3 polyunsaturated fatty acid (PUFA) in freshwater fish (Henderson and Tocher 1987). Thus, phytoplankton contain lower percentages of all long chain PUFAs, and aquatic insects contain lower percentages of 22:6n3, compared to the lipids of fish consuming these foods (Sargent et al. 1989). Accordingly, fish such as rainbow trout which feed heavily on aquatic insects have a relatively good ability to chain elongate and desaturate EFAs and their EFA requirements can be satisfied entirely by 18:2n6 and 18:3n3 (Owen et al. 1975; Sellner and Hazel 1982; Watanabe 1982; Christiansen 1984; Bell et al. 1986; Hagve et al. 1986). On the other hand, marine piscivorous fish such as Plaice and Turbot have a poor ability to chain elongate and desaturate n-3 and n-6 PUFAs of 18 carbon chain length, presumably because they normally obtain adequate amounts of these fatty acids, and of 20:4n6, 20:5n3, and 22:6n3 in their diet (Owen et al. 1972,1975). Such fish have been found to require specific individual PUFAs, notably 20:5n3 and 22:6n3 at certain minimum levels in their diet to meet their EFA requirements (Owen et al. 1972,1975).

The impact of seasonal changes in dietary fatty acid composition is likely to be greatest in piscivorous fish because they have relatively poor abilities to modify dietary EFAs. The dietary fatty acid composition of piscivorous fish can change considerably depending on the representation of different prey species in the diet. The fatty acid composition of prey species is expected to differ because proportions of NLs (poor in PUFAs) and PLs (rich in PUFAs) vary markedly between different fish species (Henderson and Tocher 1987).

The present study compares the fatty acid composition of female pike with that of their principle prey species to facilitate evaluation of the role of diet in the seasonal fatty acid dynamics of pike.

Materials and Methods

Adult pike in Lac Ste. Anne are entirely piscivorous and their diet consists predominantly of yellow perch (*Perca flavescens*), white sucker (*Catostomus commersoni*), burbot (*Lota lota*), and spottail shiner (*Notropis hudsonius*), which together comprise 94 % of total dietary caloric content (Diana 1979). Whitefish (*Coregonus clupeaformis*), walleye (*Stizostedion vitreum*), and other pike comprise the remainder of the pikes diet (Diana 1979). For the present study, adult female pike and their principle prey species were sampled from Lac Ste. Anne in June and August 1989. Attempts to capture prey species using gill nets were also made in January 1989 but only pike and adult female yellow perch were caught at this time. In June and August, pike, white sucker, and whitefish were collected using gill nets whereas juvenile perch, spottail shiner and burbot were collected by seining or dip netting in shallow water along shore. A description of the pike and prey species collected and the tissues analyzed for fatty acid content is given in Table V-1. In the case of small prey items such as juvenile perch, spottail shiner and burbot, lipids were extracted from the whole fish. For each pike, and prey item too large to homogenize whole, the major organs and tissues were sampled and whole body fatty acid composition was calculated after summing the content of each fatty acid in all organs and tissues analyzed.

Fish collected using gill nets were kept in a freezer (-20°C) prior to lipid extraction from tissues which was completed within 4 to 5 hours after removal of fish from the nets. Smaller prey species were kept alive in lake water until lipid extraction. Lipid extraction was done by homogenizing whole fish or tissue samples with 40 volumes of chloroform/methanol (Folch et al. 1957) containing BHT at levels of approximately 0.1 % of the lipid content of the extract. Lipid extracts were cleared of particulate matter by filtering through Whatman # 1 filter paper, bubbled with nitrogen, and stored in completely filled glass vials (at -30°C) prior to further processing. The washing procedure of Folch et al. 1957 (using 0.58 % NaCl) was used to remove non-lipids from the chloroform-methanol extracts.

Fatty acid analyses were performed separately on the neutral and polar lipid fractions of muscle from pike collected in January and August. Procedures used to separate neutral and polar lipids and the use of internal standards to quantify fatty acids in these fractions are described in chapter III. In all other tissues, fatty acid analysis was performed on total lipids. A known weight of tri-O-tridecanoylglycerol was added to the washed lipid extract to serve as an internal standard for quantifying fatty acids in total tissue lipids. Saponification of lipids, methylation of fatty acids and gas chromatographic determination of tissue fatty acid content and percent composition were performed as described in chapter III. Quantities of 14:0

could not be accurately measured because this fatty acid co-eluted with BHT during gas chromatography.

The prey species composition of the diet of female pike in Lac Ste. Anne during June and August are given by Diana (1979) and were used to estimate diet fatty acid composition. Diana (1979) gives data on the percentage of the pike's caloric intake contributed by different prey species and each prey species' caloric equivalent (cal/g dry wt) and dry wt:wet wt ratio. These data were used to calculate the percentage contribution of each prey species to the pike's diet on a wet wt basis (Table V-2). The fatty acid concentration (% wet wt) of each prey species and its contribution to diet wet wt were used to calculate each prey species' contribution to diet fatty acid content (Table V-2). Finally, diet fatty acid composition was calculated by weighting each prey species' fatty acid composition according to that species' contribution to diet fatty acid content.

Results

The various prey species eaten by pike differed considerably in fatty acid content. Therefore, the contribution of each prey species to the fatty acid content of the pike's diet differed somewhat from its contribution to the diet calculated on the basis of weight. This was most evident for white sucker, which contributed relatively less to diet fatty acid content than to diet weight, and for yellow perch, which in August contributed relatively more to diet fatty acid content than to diet weight (Table V-2).

In January, pike lipids contained percentages of MUFAs which were 10 wt % higher and percentages of n-3 and n-6 fatty acids which were 6 wt % and 3 wt % respectively, lower than those in lipids of adult perch (Fig. V-1). The individual fatty acids which contributed most (> 3 wt %) to the differences in fatty acid composition between pike and perch were 16:1n7 and 18:1n9, which had higher percentages in pike, and 20:4n6, 20:5n3, and 22:6n3, which were relatively more abundant in perch (Table V-3). However, when used to compare the fatty acid composition of pike and their diet, these data collected in January must be interpreted with caution because pike feed more on juvenile perch than on adults, and because the fatty acid composition of perch pertains only to somatic lipids of females.

The fatty acid composition of the pike's diet was much more accurately described in June and August when a variety of prey species, of the size eaten by pike, could be collected. Calculation of dietary fatty acid composition from the average fatty acid composition of each prey species (weighted according to each species' contribution to diet fatty acid content) gave only a single estimate for dietary fatty acid composition at each collection period. This meant that the amount of variability in dietary fatty acid composition was unknown and statistical tests based on this variability could not be performed. However, some indication of the reliability of comparisons between the fatty acid composition of pike and that of their diet can be gained by comparing the data obtained in June and August (Fig. V-1; Tables V-4,5).

In both June and August, pike contained percentages of SFAs which were lower (by 3.2 to 4.3 wt %) and percentages of MUFAs which were higher (by 2.1 to 3.8 wt %) than those in dietary lipids (Fig. V-1). Percentages of n-3,n-6, and total PUFAs in pike lipids were nearly identical to those in dietary lipids (Fig. V-1).

The various prey species which were collected differed considerably in fatty acid composition, especially in the percentages of 18:1n9 and 22:6n3. For example, 18:1n9 varied from 10.1 wt % in sucker to 22.6 wt % in burbot (Table V-4) and 22:6n3 varied from 7.8 wt % in spottail shiner (Table V-5) to 24.1 wt % in sucker (Table V-4).

Individual fatty acids whose percentages in pike and dietary lipids differed by more than 2 wt % were, 16:0 (August only), 18:0 (both months), 16:1n7 (June only), 20:5n3 (both months), and 22:6n3 (both months) (Tables V-4,5). Comparison of Tables V-4 and V-5 shows that differences in the percent composition of individual fatty acids between pike and dietary lipids in June were qualitatively and quantitatively similar to the differences which existed in August. In both months, pike lipids contained lower proportions of 16:0 and 18:0 and higher percentages of 16:1n7 and 18:1n9 compared to dietary lipids (Tables V-4,5). Percentages of 18:2n6 were greater in pike than in their diet and were offset by similarly large but opposite differences in the percentage of 20:4n6 (Tables V-4,5). Compared to dietary lipids, pike contained higher percentages of 18:3n3 and 22:6n3 which were offset by reductions of similar magnitude in the percentage of 20:5n3 (Tables V-4,5).

Discussion

In June and August, when the most complete data were collected, female northern pike had a fatty acid composition which closely resembled that of their diet. The only differences among the major fatty acid classes were 3.2 to 4.3 wt % lower percentages of SFAs and 2.2 to 3.8 wt % higher percentages of MUFAs in pike compared to dietary lipids (Fig. V-1). Percentages of total n-3 and total n-6 PUFAs in pike were nearly identical to those of the diet (Fig. V-1). Among individual fatty acids the largest differences occurred in 20:5n3 which was 4.1 wt % lower and 22:6n3 which was 4.1 wt % higher in pike than in dietary lipids in June (Table V-4).

The differences in fatty acid composition between pike and their diet are quite small relative to other published comparisons of fatty acid composition between fish and their diet (Linko et al. 1985; Schauer and Simpson 1985; Muje et al. 1989). The variable degree of similarity in fatty acid composition between freshwater fish and their diet indicates that the ability to modify the fatty acid composition of dietary lipids during assimilation may vary considerably between freshwater fish species and not just between freshwater and marine fish as has been implied in the literature (Sargent et al. 1989).

The similarity in fatty acid composition between pike and their diet suggests that pike may not need to, or may not have the ability to, significantly modify the fatty acid composition of dietary lipids during their assimilation. Certainly, lower percentages of 20:4n6 and 20:5n3 in pike than in dietary lipids (Tables V-4,5) provide no evidence of significant elongation and desaturation of 18:2n6 or 18:3n3 by pike. Although percentages of 22:6n3 are higher in pike than in their diet (Tables V-4,5), this is not sufficient to indicate that pike are actively elongating and desaturating 20:5n3 to 22:6n3. Because the gross dietary conversion efficiency of pike is about 30 % (Diana 1982), pike probably consume considerably more 22:6n3 (and other nutrients) than they accumulate in their tissues. Therefore, higher percentages of 22:6n3 in pike compared to their diet can be due to selective retention of this fatty acid and does not imply that pike are synthesizing 22:6n3 from 20:5n3.

Quantities of n-3 PUFAs present in the pike's diet equal or exceed the maximum dietary requirements for these essential fatty acids which have been established experimentally in better studied species such as rainbow trout. Assuming the water content of the pike's diet to be similar to that of yellow perch (78 % of wet wt; Tanasichuk and Mackay 1989), then the total n-3 PUFA content of the pike's diet is about 1.4 % of dry weight. This falls within the dietary n-3 PUFA requirements (0.8 to 1.7 % of dry wt) established experimentally in rainbow trout (Castell et al. 1972; Watanabe et al. 1974). However, the EFA requirements of fish vary according to the quantity of lipid and the type of fatty acid (ie: 18 carbon vs long chain PUFA) supplied in the diet. Accordingly, the n-3 PUFA requirements of rainbow trout have also been expressed as 20 % of dietary fatty acids if supplied as 18:3n3 and as 10 % of dietary fatty acids if supplied as 20:5n3 plus 22:6n3 (Takeuchi and Watanabe 1977). Percentages of total n-3 PUFAs (29.1 to 40.1; Tables V-3,4,5) in the pike's diet exceed the requirements of rainbow trout expressed as 18:3n3. Percentages of 20 and 22 carbon n-3 PUFAs in the pike's diet (25.5 to 38.3; Tables V-3,4,5) are double or triple the requirements established for trout. Although quantities of n-3 PUFAs four times in excess of dietary requirements suppress growth in trout (Takeuchi and Watanabe 1979), the high percentage of n-3 PUFAs in the diet of pike does not appear to be detrimental because pike in Lac Ste. Anne exhibit normal growth rates (Mackay 1989) and otherwise appear healthy. This may indicate that dietary requirements for long chain n-3 PUFAs are higher in pike than in rainbow trout. On the whole, there is good agreement between the n-3 PUFA content of the pike's natural diet and experimentally derived n-3 requirements of freshwater fish. This suggests that natural foods can be useful indicators of the optimal composition of fish diets.

Total fatty acid content and percent composition exhibited considerable variation between different prey species and temporal variation within a single species (Tables V-4,5). The potential exists for pike to experience similarly large temporal variations in diet composition if they feed exclusively on a single prey species or if they switch from eating predominantly juvenile yellow perch to eating one of the other prey species. However, the strategy of feeding on several prey species may allow pike to reduce the amount of temporal variation in diet fatty acid composition they have to deal with.

It has been suggested that north-temperate fish may be able to increase their dietary lipid intake in winter, and thus help satisfy the requirements of fatty acids for ovary growth by feeding on adult individuals, especially females, of prey species which also undergo gonad maturation over winter. However, lipids of mature ovaries of yellow perch and burbot consist predominantly of wax esters which are considerably less digestible than triacylglycerols and polar lipids (Henderson and Tocher 1987). The low digestibility of wax esters, together with the low fatty acid content (0.56 % wet wt; Table V-3) of somatic tissues of yellow perch, suggests that female perch with mature ovaries may not provide greatly increased quantities of fatty acids to pike over winter.

In summary, it appears that pike in Lac Ste. Anne have acquired a fatty acid composition which closely resembles that of dietary lipids. This suggests that pike may resemble marine piscivorous fish and terrestrial carnivores such as the cat (Davidson et al. 1990) in having relatively poor abilities to elongate and desaturate dietary EFAs and in requiring specific long chain n-3 and n-6 PUFAs in the diet. Therefore, seasonal changes in dietary fatty acid composition can be expected to significantly influence the fatty acid composition of pike. Interestingly, in a few Alberta lakes adult pike have been found to feed mostly on aquatic invertebrates such as dragonfly nymphs and freshwater shrimp (Chapman and Mackay 1990). In these waters pike may need to convert dietary 20:5n3 to 22:6n3, and if unable to do so, may experience a deficiency of 22:6n3.

Table V-1. Characteristics of pike and prey items sampled for fatty acid analysis.

Sampling Date	Species Sampled	n	Body weight (grams) (mean ± SD)	Standard Length (cm) (mean ± SD)	Tissues Analyzed
January 28-31'1989	female pike	5	1,155 ± 208	49.1 ± 3.0	ovary, liver, white muscle, adipopancreatic tissue
	female perch	6	133 ± 24	18.9 ± 1.1	liver, white muscle, viscera (includes digestive tract, adipose tissue, spleen, pancreas, but not ovary[a])
June 13-16'1989	female pike	6	1,290 ± 456	52.3 ± 6.0	liver, white muscle, adipopancreatic tissue
	white sucker	3	88 to 368	17.1 to 26.3	white muscle, viscera (includes gonads, liver, adipose tissue, and digestive tract)
	burbot	3	12 to 72	-	white muscle, viscera (includes gonads, liver, adipose tissue, and digestive tract)
	spottail shiner	6	2.6 ± 0.5	-	whole fish
	juvenile perch	8	2.7 ± 0.5	-	whole fish
August 1-8' 1989	pike	6	789 ± 209	43.9 ± 4.1	liver, white muscle, adipopancreatic tissue
	white-fish	4	214 ± 21	24.3 ± 0.8	liver, white muscle, viscera (includes gonads, adipose tissue, digestive tract)
	burbot	9[b]	1.7 ± 0.4	-	whole fish
	spottail shiner	8	2.8 ± 1.1	-	whole fish
	juvenile perch	8	4.4 ± 0.6	-	whole fish

a - ovarian lipids of perch are predominantly wax esters which precluded fatty acid analysis

b - to obtain enough tissue for analysis, the six smallest burbot were homogenized in pairs, giving a total of six replicates.

Table V-2. Contribution of various prey species to the wet weight and fatty acid content of the northern pike diet in Lac Ste. Anne.

Prey species	Sampling Date					
	June			August		
	FA conc.[a] % wet wt (mean ± SE)	% of diet[b] wet wt	% of dietary[c] FA content	FA conc.[a] % wet wt (mean ± SE)	% of diet[b] wet wt	% of dietary[c] FA content
Yellow Perch	1.09 ± 0.13	51.1	51.1	1.42 ± 0.12	57.7	71.0
White Sucker	0.66 ± 0.04	22.1	13.4	----	23.9	13.8[d]
Spottail shiner	1.45 ± 0.16	12.7	16.9	2.49 ± 0.34	0	0
Burbot	1.54 ± 0.61	11.9	16.8	0.98 ± 0.01	11.8	10.1
Whitefish	----	2.2	1.8[d]	0.89 ± 0.08	6.6	5.1
Total		100.0	100.0		100.0	100.0

a - total fatty acid concentration of each prey species

b - the contribution of each prey species to the pike's diet, expressed as a percentage of diet wet weight and calculated from data given by Diana (1979). In August, walleye and pike together comprised about 6 % of the pike's diet (Diana 1979), but were not included in the present analysis.

c - the contribution of each prey species to the pike's total dietary intake of fatty acids was calculated from the fatty acid concentration of each prey species and that species' percentage contribution to diet wet weight

d - calculated using the fatty acid concentration of sucker in June and that of whitefish in August because these were the only dates on which sucker and whitefish were caught

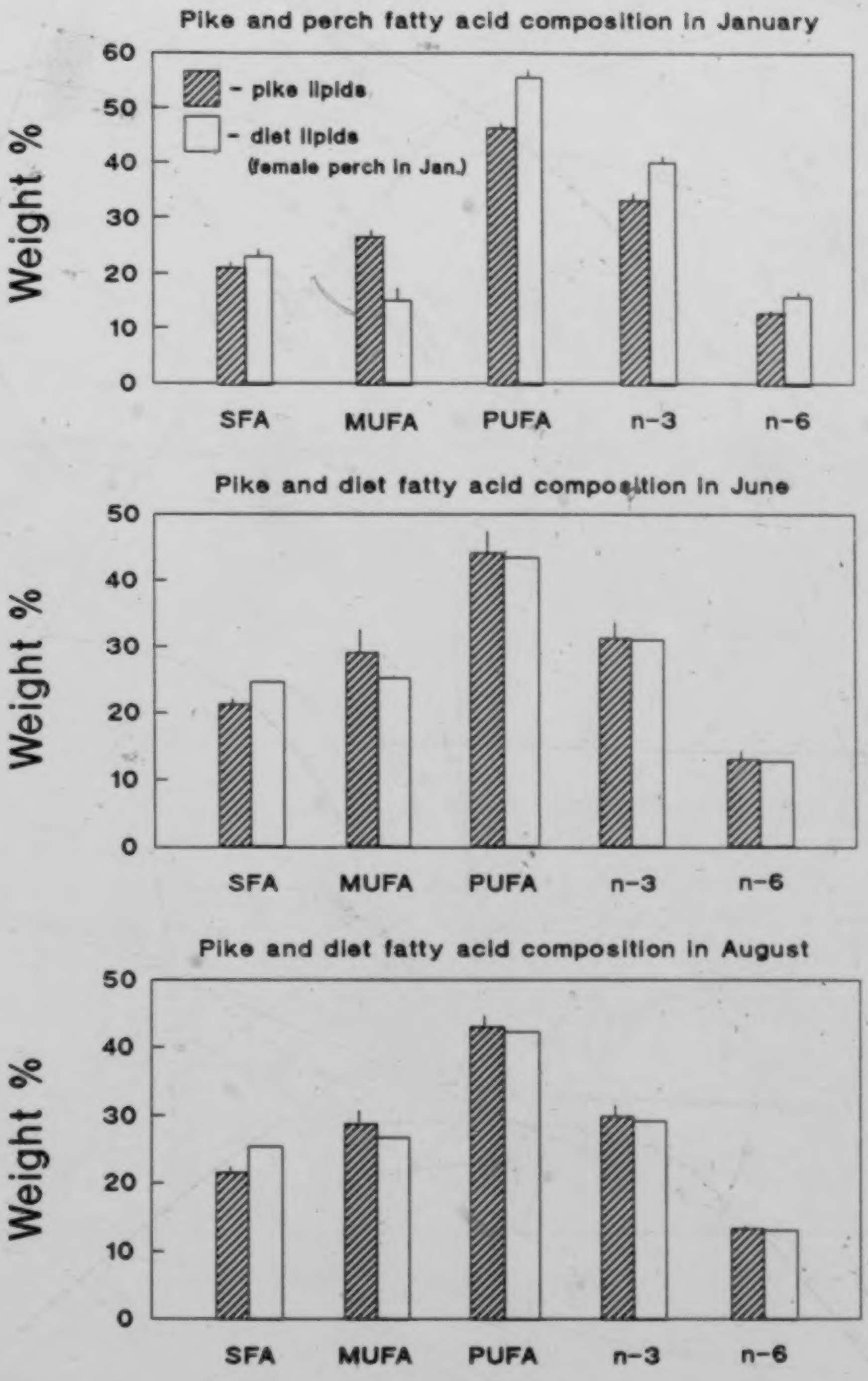

Figure V-1. Fatty acid composition of pike and their diet. Quantities of fatty acids (ie: wt %) are expressed as a percentage of the total weight of fatty acids in dietary lipids or in the total lipids of pike tissues. Sample sizes are given in Tables V-3 to V-5. Vertical bars represent 95 % C.I.'s. In June and August C.I.'s could not be calculated for diet data.

Table V-3. Fatty acid compositions of pike and yellow perch in January.[a] Data are given as mean ± SE

Fatty Acid	Pike (n=5)	Yellow perch (n=6)
16:0	16.2 ± 0.18[b]	17.0 ± 0.39
18:0	5.5 ± 0.06	6.7 ± 0.10
16:1n7	10.4 ± 0.37	5.8 ± 0.38
18:1n9	16.3 ± 0.18	9.8 ± 0.56
18:2n6	5.0 ± 0.22	2.4 ± 0.17
20:4n6	6.3 ± 0.17	10.5 ± 0.36
22:5n6	1.6 ± 0.04	3.1 ± 0.17
18:3n3	3.4 ± 0.17	1.9 ± 0.14
20:5n3	5.8 ± 0.05	8.8 ± 0.40
22:5n3	1.9 ± 0.04	2.6 ± 0.26
22:6n3	22.2 ± 0.64	26.9 ± 0.62
others	5.4 ± 0.10	4.7 ± 0.24
SFA	21.7 ± 0.21	23.7 ± 0.36
MUFA	26.7 ± 0.50	15.5 ± 0.94
PUFA	46.3 ± 0.49	56.1 ± 0.63
all n-6	12.9 ± 0.08	16.0 ± 0.35
all n-3	33.3 ± 0.51	40.1 ± 0.64
FA conc. % wet wt	1.31 ± 0.064	0.56 ± 0.021

a - fatty acid compositions of pike and perch were estimated from weighted averages of the compositions of the individual organs and tissues identified in Table V-1.

b - fatty acid compositions are expressed as the mean weight % of the indicated fatty acids in total lipids of pike and perch

Table V-4. Fatty acid compositions of pike, the pike's diet, and prey species in June.[a] Data are given as mean ± SE.

Fatty Acid	Pike (n=6)	Pike diet[b]	Yellow perch (n=8)	Sucker (n=3)	Burbot (n=3)	Shiner (n=6)
16:0	15.3 ± 0.15[c]	16.4	16.1 ± 0.21	18.6 ± 0.21	15.5 ± 0.35	16.7 ± 0.46
18:0	5.9 ± 0.15	8.0	7.9 ± 0.32	7.5 ± 0.40	8.4 ± 1.35	8.2 ± 0.28
16:1n7	11.4 ± 0.46	9.4	9.5 ± 0.66	8.4 ± 0.22	9.6 ± 1.88	9.9 ± 0.60
18:1n9	17.6 ± 1.26	15.7	14.9 ± 1.09	10.1 ± 0.22	22.6 ± 3.15	16.1 ± 0.70
18:2n6	5.4 ± 0.28	3.7	3.6 ± 0.27	2.8 ± 0.13	3.9 ± 0.41	4.7 ± 0.50
20:4n6	5.9 ± 0.22	7.2	6.9 ± 0.25	7.4 ± 0.33	8.9 ± 1.76	6.6 ± 0.39
22:5n6	1.7 ± 0.09	1.9	2.4 ± 0.17	2.1 ± 0.20	1.0 ± 0.14	0.9 ± 0.05
18:3n3	3.7 ± 0.17	2.7	2.1 ± 0.22	2.1 ± 0.06	3.6 ± 0.44	4.0 ± 0.53
20:5n3	5.6 ± 0.12	9.7	9.5 ± 0.30	9.0 ± 0.50	11.0 ± 1.26	9.7 ± 0.45
22:5n3	2.0 ± 0.08	2.6	2.2 ± 0.06	3.8 ± 0.11	2.9 ± 0.20	2.8 ± 0.18
22:6n3	19.8 ± 1.20	15.7	16.4 ± 1.13	24.1 ± 0.66	8.0 ± 1.47	14.0 ± 1.24
others	5.7 ± 0.14	6.9	8.5 ± 0.37	4.0 ± 0.25	4.7 ± 0.15	6.4 ± 0.38
SFA	21.2 ± 0.14	24.4	24.0 ± 0.48	26.1 ± 0.19	23.8 ± 1.02	24.9 ± 0.67
MUFA	29.0 ± 1.51	25.2	24.5 ± 1.66	18.6 ± 0.43	32.2 ± 5.02	25.9 ± 1.29
PUFA	44.1 ± 1.45	43.5	43.0 ± 1.31	51.3 ± 0.34	39.3 ± 4.15	42.7 ± 1.04
all n-6	13.0 ± 0.42	12.8	12.9 ± 0.28	12.3 ± 0.11	13.7 ± 1.66	12.2 ± 0.22
all n-3	31.1 ± 1.09	30.7	30.1 ± 1.16	38.9 ± 0.34	25.5 ± 2.49	30.5 ± 1.10
FA conc. % wet wt	0.93 ± 0.084	1.09	1.09 ± 0.125	0.66 ± 0.037	1.54 ± 0.607	1.45 ± 0.164

a - fatty acid compositions of pike and prey species were estimated from weighted averages of the compositions of the individual organs and tissues identified in Table V-1.

b - the fatty acid composition of the pike's diet was calculated from the contribution of each prey species to the pike's dietary fatty acid intake as indicated in Table V-2.

c - fatty acid compositions are the mean weight % of the indicated fatty acids in total lipids of pike, the pike's diet, and prey species

Table V-5. Fatty acid compositions of pike, the pike's diet, and prey species in August.[a]
Data are given as mean ± SE.

Fatty Acid	Pike (n=6)	Pike diet[b]	Yellow perch (n=8)	Burbot (n=6)	Shiner (n=8)	Whitefish (n=4)
16:0	14.9 ± 0.23[c]	17.0	16.8 ± 0.29	16.4 ± 0.23	17.6 ± 0.32	16.3 ± 0.46
18:0	6.4 ± 0.14	8.6	8.7 ± 0.27	10.6 ± 0.13	8.1 ± 0.32	6.1 ± 0.10
16:1n7	11.3 ± 0.28	10.9	11.9 ± 0.67	7.8 ± 0.13	12.8 ± 0.47	8.6 ± 0.74
18:1n9	17.6 ± 0.38	15.9	17.0 ± 0.43	17.4 ± 0.18	21.3 ± 0.66	13.5 ± 0.82
18:2n6	5.7 ± 0.11	4.4	4.9 ± 0.27	3.5 ± 0.10	6.5 ± 0.37	4.3 ± 0.36
20:4n6	5.8 ± 0.16	7.0	6.7 ± 0.37	9.6 ± 0.15	5.2 ± 0.39	4.9 ± 0.23
22:5n6	1.8 ± 0.05	1.6	1.6 ± 0.10	1.1 ± 0.03	0.9 ± 0.07	1.8 ± 0.14
18:3n3	4.3 ± 0.23	3.7	3.9 ± 0.28	3.2 ± 0.06	5.0 ± 0.29	5.4 ± 0.51
20:5n3	6.2 ± 0.15	9.5	9.4 ± 0.29	11.2 ± 0.26	6.9 ± 0.34	8.6 ± 0.38
22:5n3	2.6 ± 0.05	2.3	1.8 ± 0.09	3.2 ± 0.07	2.1 ± 0.10	3.6 ± 0.10
22:6n3	16.7 ± 0.78	13.7	11.8 ± 0.79	10.1 ± 0.21	7.8 ± 0.62	18.2 ± 1.95
others	6.8 ± 0.43	5.4	5.4 ± 0.22	5.7 ± 0.10	5.8 ± 0.16	8.6 ± 0.62
SFA	21.3 ± 0.36	25.6	25.5 ± 0.43	27.0 ± 0.22	25.8 ± 0.39	22.4 ± 0.46
MUFA	28.9 ± 0.64	26.8	29.0 ± 1.03	25.3 ± 0.28	34.1 ± 0.99	22.2 ± 1.51
PUFA	43.1 ± 0.68	42.2	40.2 ± 0.95	42.0 ± 0.18	34.3 ± 0.87	46.8 ± 1.64
all n-6	13.3 ± 0.16	13.1	13.2 ± 0.39	14.3 ± 0.24	12.6 ± 0.21	11.0 ± 0.25
all n-3	29.8 ± 0.69	29.1	26.9 ± 0.71	27.7 ± 0.35	21.8 ± 0.81	35.8 ± 1.70
FA conc. % wet wt	1.39 ± 0.100	1.15	1.42 ± 0.120	0.98 ± 0.013	2.49 ± 0.342	0.89 ± 0.083

a - fatty acid compositions of pike and prey species were estimated from weighted averages of the compositions of the individual organs and tissues identified in Table V-1.

b - the fatty acid composition of the pike's diet was calculated from the contribution of each prey species to the pike's dietary fatty acid intake as indicated in Table V-2.

c - fatty acid compositions are the mean weight % of the indicated fatty acids in total lipids of pike, the pike's diet, and prey species

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Chapter VI

The effect of acclimation temperature on fatty acid composition of liver and white muscle in northern pike (*Esox lucius* L.).

Introduction

The seasonal effects of temperature on tissue fatty acid composition in north-temperate fish are not well understood. There are several reasons for this. First, previous studies have interpreted temperature related changes in tissue fatty acid composition of fish primarily as adaptations to maintain the proper physical state of membrane and storage lipids (Cossins et al. 1977; Cossins and Prosser 1982; Hazel 1979a,b,1984,1989). However, the indirect effects of temperature on tissue fatty acid composition through changes in fish growth rate, food intake, and in the fatty acid composition of prey species has not been examined. Second, north-temperate fish experience seasonal cycles in ovarian recrudescence, food intake, and diet composition independently of temperature (Medford and Mackay 1978; Diana 1979; Diana and Mackay 1979; Love 1980; Chapman and Mackay 1990) and these may modify the changes in tissue fatty acid composition which occur in response to temperature cycles. Consequently, it is not known whether wild fish respond to seasonal temperature cycles with the same changes in fatty acid composition which they exhibit in response to temperature acclimation in the laboratory.

Previous chapters have described the timing and magnitude of seasonal changes in the tissue fatty acid composition of female northern pike (chapters II and III) and the role of ovarian recrudescence in these cycles (chapter IV). The present chapter examines the role of temperature in the seasonal fatty acid dynamics of pike. The experiment was designed so that the effects of temperature on tissue fatty acid composition could be expressed not only in terms of the homeoviscous adaptation response but also through changes in the pike's growth rate, food intake, and diet fatty acid composition.

Materials and Methods

Young of the year (YOY) pike were used in this study because adult pike do not readily feed and grow in captivity. The 14 YOY pike used for this study were collected by seining from Baptist Lake (54° 45′ N, 113° 33′ E), Alberta in late September 1988 and transported within two days to the University of Alberta aquatic facilities where they were held in 400 L tanks. For the first two weeks of captivity all pike were held at between 12 and 14°C. Pike were then weighed and seven individuals allocated to each of a warm (21°C) and a cold (6°C) acclimation group. Pike were allowed to acclimate to these temperatures for 49 days. One of the warm acclimating pike died from unknown causes during this period. At the start of temperature acclimation, the two groups of pike did not differ significantly (t-test, $p < 0.05$) in body weight which averaged 81 ± 14 g (mean ± SD, $n=6$) in the warm acclimation group and 90 ± 17 g (mean ± SD, n=7) in the cold acclimation group. The photoperiod regime was 12 h light: 12 h dark during the entire experimental period.

Both groups of pike had continual access to food in the form of juvenile yellow perch (Perca flavescens) which had been collected from Lac Ste. Anne and housed together with the pike and thus also underwent temperature acclimation. Active feeding of both groups of pike was confirmed by visual observation and the presence of perch in pike stomachs at the end of the acclimation period.

At the end of the acclimation period, pike were sacrificed, weighed again, and a 2 g strip of epaxial white muscle and the entire liver were excised from each pike and frozen in dry ice for later fatty acid analysis. Extraction of lipids from frozen whole liver and muscle samples and removal of non-lipids were done using the method of Folch et al. (1957). Separation of neutral and polar lipids was achieved using the silicic acid chromatography method of Rouser et al. 1967. The method of Bannon et al. (1982) was used to saponify the purified lipids and methylate fatty acids. Fatty acid analysis was done with gas chromatography using authentic standards (MaxEpa oil) to identify individual fatty acids.

The liver NLs of these pike contained considerable quantities of unidentified compounds (probably furan fatty acids - Glass et al. 1974) which co-eluted with many of the PUFAs. Quantification of PUFAs in liver neutral lipids required separation of these fatty acids from the unidentified compounds which was achieved using the argentation chromatography procedure of Glass et al. (1977). A complete description of the methods used in this study for extraction and purification of lipids, and quantification of fatty acids is given in chapter III.

Results

Over the seven week experiment, warm acclimating pike grew in body weight by 50 % whereas the average weight of the cold acclimating pike remained constant (Fig. VI-1). At the end of the experiment, liver weights (expressed relative to carcass weight) were about 29 % greater in cold acclimated pike than in warm acclimated ones (Fig. VI-1). Warm and cold acclimated pike had concentrations of NLFAs in their muscle (about 0.027 % of tissue wet wt) which were very low compared to those of adult wild pike in central Alberta (0.4 to 0.7 %; Fig. II-2) but similar to those of adult pike in the arctic (0.04 %; Table IV-1). When sacrificed, cold acclimated pike had concentrations and total amounts of NLFAs in their liver which were only 24 % and 28 % respectively of the levels found in warm acclimated pike (Fig. VI-1). Both the concentration and content of PLFAs in pike white muscle were significantly increased as a result of cold acclimation (Fig. VI-1). Acclimation temperature had no effect on the PLFA concentration of liver, but because of their relatively larger livers, cold acclimated pike contained about 20 % more PLFAs in their livers compared to warm acclimated pike (Fig. VI-1).

Changes in the fatty acid composition of liver NLs which resulted from cold acclimation included a 4 wt % decrease in the percentage of SFAs, an 7 wt % increase in MUFAs, and a trend toward lower percentages of n-3 fatty acids (Fig. VI-2). Due to the presence of unidentified compounds, quantities of 20:4n6, 18:3n3, and 20:5n3 in muscle NLs could not be measured. Percentages of the major fatty acid groups, calculated from those fatty acids which were quantified in muscle NLs, did not differ significantly between warm and cold acclimated pike (Fig. VI-2).

Cold acclimation significantly reduced the percentage of SFAs in PLs of both muscle and liver (Fig. VI-2). In liver PLs, increased unsaturation at low temperature resulted from about equally large increases in the percentages of MUFAs and n-3 fatty acids. Increased unsaturation of muscle PLs at low temperature resulted solely from increases in the percentage of n-3 fatty acids which were sufficiently large to more than offset a significant decline in the percentage of n-6 fatty acids (Fig. VI-2).

Of the two major SFAs in liver NLs, only the percentage of 16:0 declined significantly as a result of cold acclimation (Table VI-1). Cold acclimation produced significant and approximately equal elevations in the percentages of 16:1n7 and 18:1n9 in liver NLs (Table VI-1). Among the PUFAs in liver NLs, the percentages of 18:2n6 and 18:3n3 increased significantly during cold acclimation, whereas percentages of most of the others (20:4n6, 20:5n3, 22:5n3, and 22:6n3) decreased. None of the individual fatty acids in muscle NLs exhibited large and significant differences in % composition between cold and warm acclimated pike (Table VI-1).

Cold induced reductions in the percentage of total SFAs in liver PLs (Fig. VI-2) were primarily due to changes in the percentage of 16:0 (Table VI-2). In muscle PLs, percentages of 16:0 and 18:0 exhibited approximately equal reductions with cold acclimation, but only the change in 18:0 was statistically significant. Percentages of 16:1n7 increased with cold acclimation in PLs of both liver and muscle, but this produced significant changes in the percentage of MUFAs only in liver PLs (Table VI-2).

Due to the presence of unidentified compounds, the percentage of 18:3n3 in liver PLs could not be quantified. Of the PUFAs which were quantified in liver PLs, only the percentages of 20:5n3 and 22:5n3 were significantly influenced by temperature acclimation and were higher in cold acclimated than in warm acclimated pike (Table VI-2). In muscle PLs, cold acclimation elevated the percentage of 18:2n6, but because of larger reductions in the percentage of 20:4n6 (Table VI-2), the total percentage of n-6 fatty acids was also significantly lower in cold acclimated pike (Fig. VI-2). Higher total percentages of n-3 fatty acids in muscle PLs of cold acclimated pike than in warm acclimated ones were due to changes in 18:3n3 and 22:6n3 (Table VI-2).

Discussion

Juvenile pike were used for this experiment so that the seasonal effects of temperature on growth rate and dietary fatty acid composition could be simulated. This would be difficult to do with adult pike. Accordingly, the 50 % increase in body weight exhibited by the warm acclimated pike during the experiment is similar to the amount of growth experienced during summer (May to September) by adult pike in Lac Ste. Anne (Billard et al. 1983). Lack of significant growth by the cold acclimated pike resembles the condition of wild female pike during winter because the latter fish grow by only about 5 % in somatic wt from September to March (Billard et al. 1983).

Concentrations of NLFAs and PLFAs in liver and PLFAs in muscle of juvenile pike were also similar to those of wild pike. However, concentrations of NLFAs in muscle were much lower in both groups of juvenile pike than in adult Lac Ste. Anne pike. This difference may be related to age because young, actively growing animals usually direct more nutrients to body growth and less to energy storage compared to older animals (Love 1980).

An increase in liver weight during cold acclimation appears to be a general phenomenon in fish, being observed in pike in this study and in other fish species (Hazel 1979b; Prosser 1986). Because larger livers can perform a greater total quantity of metabolic work, an increased hepatosomatic index in the cold may be part of the temperature adaptation response (Holeton 1974; Hochachka and Somero 1973) whereby fish attempt to compensate for the reduced metabolic rate imposed on them by low temperature. The results obtained in chapter IV, together with studies on the effects of estrogen hormones in fish (van Bohemen et al. 1982; Ng et al. 1984; Mommsen and Walsh 1988), suggest that ovarian recrudescence may also increase liver weight in fish. The purpose of this response would be to increase vitellogenin production in the liver. Thus, the increase in liver weight which occurs in pike during late summer and early winter in Lac Ste. Anne (Fig. II-1) likely results from the combined effects of declining temperature and ovarian recrudescence.

Cold acclimation greatly decreased NLFA concentrations in liver and significantly increased PLFA concentrations in muscle (Fig. VI-1). As shown in chapter IV, ovarian recrudescence does not appear to affect either of these parameters. This suggests that the significant declines in liver NLFA concentrations which occur from June to January and increases in muscle PLFA concentrations between July and September in wild pike (Fig. II-2) are primarily responses to temperature, or some factor (food intake, growth rate, diet fatty acid composition) correlated with temperature.

The influence of temperature on liver NLFA concentrations in the laboratory (this chapter) and in the wild (chapter II) is probably an indirect one resulting from changes in the rate of food intake. At high temperatures, and during spring and summer, pike feed actively (Diana 1979) with the result that lipids absorbed from the gut may need to be temporarily stored in the liver before they can be incorporated into the appropriate plasma lipoproteins for export to other tissues. Increased concentrations of PLFAs in pike muscle with cold acclimation probably reflect a proliferation of mitochondrial and sarcoplasmic reticulum membranes. The physiological advantage of mitochondrial proliferation in the cold is thought to be a reduced intracellular diffusion distance for oxygen (Tyler and Sidell 1984; Egginton and Sidell 1989). A proliferation of sarcoplasmic reticulum membranes is thought to facilitate calcium diffusion to the contractile proteins (Penny and Goldspink 1980).

The effects of temperature on organelle proliferation is the most likely explanation for the seasonal changes in muscle PLFA content observed in Lac Ste. Anne pike because ovarian recrudescence does not influence muscle PLFA content (chapter IV) and because there appears to be no reason why other factors such as food intake, diet composition or growth rate should influence this parameter. Therefore, it is noteworthy that Lac Ste. Anne pike completed their seasonal increases in muscle PLFA concentrations by September (Fig. II-2), long before winter water temperatures were attained. This suggests that in the wild, pike may use factors other than temperature, probably photoperiod, as an environmental cue to anticipate, and initiate membrane proliferation in advance of, declining temperature.

In liver NLs, cold acclimation significantly increased the percentage of MUFAs, decreased the percentage of n-3 PUFAs (although less convincingly), and caused reciprocal changes in 18:2n6 and 18:3n3 versus long chain PUFAs (Fig. VI-2; Table VI-1). Very similar changes accompanied ovarian recrudescence in arctic pike (chapter IV). These results suggest that the increases in MUFAs, decreases in n-3 PUFAs, and reciprocal changes in 18 carbon versus long chain PUFAs which occur in liver NLs of wild pike during late summer and early winter (Figs. III-4,9) are due to the combined effects of cold acclimation and ovarian recrudescence. Cold acclimation also reduced the percentage of SFAs in liver NLs of juvenile pike (Fig. VI-2), but this change was not produced by ovarian recrudescence (chapter IV), nor did it occur seasonally in wild adult pike (chapter III). This may reflect a difference in the way juvenile and adult pike respond to temperature change or may indicate that in wild pike declines in the percentage of SFAs in liver NLs during cold acclimation are masked by the effects of ovarian recrudescence or dietary changes.

Seasonal changes which wild pike experience in the fatty acid composition of liver PLs include increases in the percentage of MUFAs, and decreases in the percentage of SFAs and n-3 PUFAs during early winter (Fig. III-6). Similar changes in the percentage of SFAs and MUFAs in liver PLs of pike can be induced by cold acclimation (Fig. VI-2) but not by ovarian recrudescence (Fig. IV-2). Hence, seasonal changes in the percentage of SFAs and MUFAs in liver PLs of wild pike are probably due primarily to temperature, perhaps as a homeoviscous adaptation response. However, decreases in the percentage of n-3 PUFAs in liver PLs of wild pike during early winter are probably due mainly to ovarian recrudescence (Fig. IV-2), because cold acclimation increases, rather than decreases, the percentage of n-3 PUFAs (Fig. VI-2).

Cold acclimation and ovarian recrudescence also had largely opposite effects on the fatty acid composition of muscle PLs. Cold acclimation increased the percentage of n-3 PUFAs, and decreased percentages of SFAs and n-6 PUFAs (Fig. VI-2). Ovarian recrudescence appeared to decrease the percentage of n-3 PUFAs, increase the percentage of n-6 PUFAs, and had no effect on percentages of SFAs (Fig. IV-2). In Lac Ste. Anne pike, seasonal changes in the fatty acid composition of muscle PLs more closely resemble the effects of temperature change than ovarian recrudescence: during early winter percentages of SFAs decrease while percentages of n-3 PUFAs increase (Fig. III-7).

In the muscle PLs of adult wild pike, 16:0 undergoes the largest and most clearly defined seasonal changes of any fatty acid (Fig. III-14). However, in juvenile pike, 18:0, 20:4n6, and 22:6n3 also undergo relatively large changes in percent composition in response to cold acclimation (Table VI-2). Again, it is tempting to speculate that in wild fish the effects of ovarian recrudescence may alter the changes in fatty acid composition which the fish would otherwise show in response to temperature acclimation.

From the results presented in this chapter, many of the seasonal changes in fatty acid content and percent composition of liver and muscle of wild pike resemble, and perhaps can be attributed to, the direct and indirect effects of temperate change. Some of the effects of cold acclimation, particularly changes in liver wt and liver NL fatty acid composition resemble the effects of ovarian recrudescence. Hence in wild pike, cold acclimation and ovarian recrudescence may act synergistically on some physiological parameters. Other effects of cold acclimation, such as changes in the fatty acid composition of muscle PLs and in the percentage of n-3 PUFAs in liver PLs, appear to be opposite to the effects of ovarian recrudescence. Future studies on the effects of environmental and physiological factors on fish fatty acid composition should consider these types of interactions when describing the significance of experimental findings to natural populations.

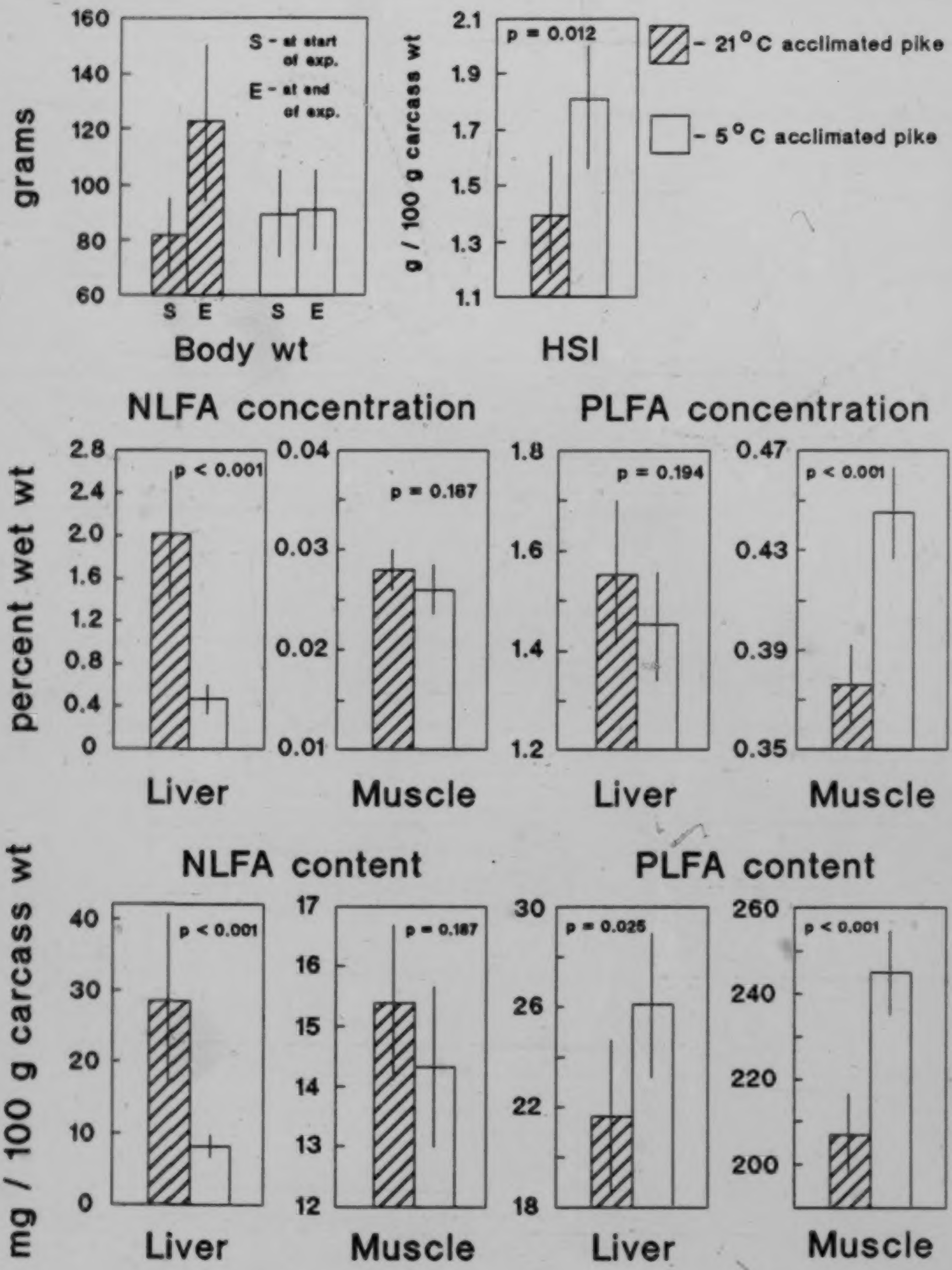

Figure VI-1. Effect of acclimation temperature on the body weight, hepatosomatic index (HSI), and tissue fatty acid content of pike. Means and 95 % C.I.'s are shown. Samples size is 6 for warm acclimated pike and 7 for cold acclimated pike. P values indicate the significance of differences between warm and cold acclimated pike (t-test for unbalanced designs).

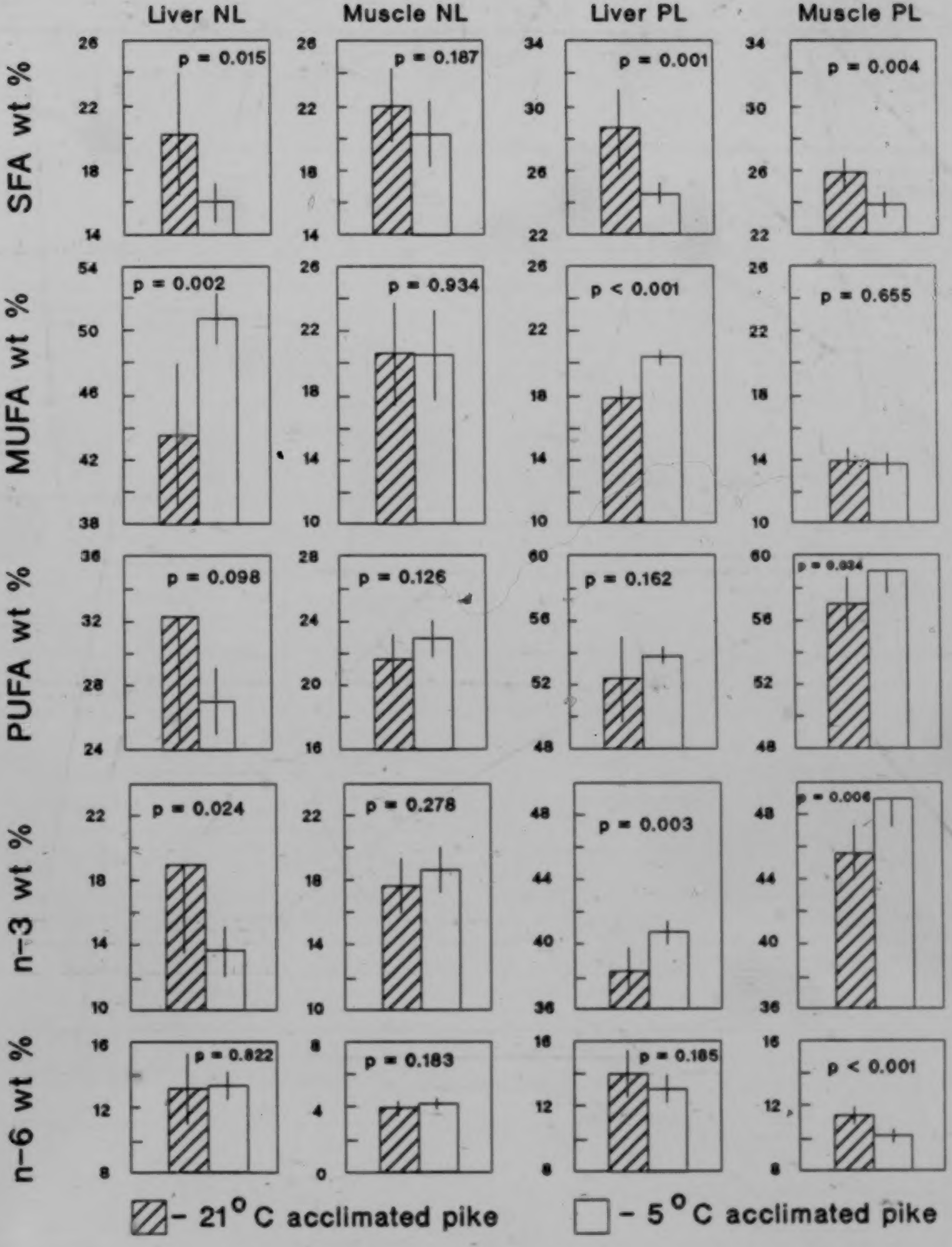

Figure VI-2. Effect of acclimation temperature on the percentages of major fatty acid groups in the neutral lipids (NL) and polar lipids (PL) of pike liver and muscle. Other details as in Figure VI-1.

Table VI-1. Effect of acclimation temperature on the fatty acid composition of neutral lipids in pike white muscle and liver. Data are given as mean ± SE.

Fatty Acid	Liver				Muscle			
	p value[c]	$\|A-B\|$[b]	21°C (A) (n=6)	6°C (B) (n=7)	p value[c]	$\|C-D\|$[b]	21°C (C) (n=6)	6°C (D) (n=7)
16:0	0.005	4.6	12.4 ± 1.37[a]	7.8 ± 0.32	0.186	1.3	13.4 ± 0.63	12.1 ± 0.59
18:0	0.380	0.4	7.8 ± 0.32	8.2 ± 0.26	0.255	0.5	8.6 ± 0.34	8.1 ± 0.30
16:1n7	< 0.001	3.8	12.0 ± 0.74	15.8 ± 0.39	0.785	0.1	6.5 ± 0.28	6.6 ± 0.29
18:1n9	0.009	3.4	31.6 ± 1.02	35.0 ± 0.46	0.853	0.2	14.1 ± 1.00	13.9 ± 0.92
18:2n6	< 0.001	2.3	5.7 ± 0.22	8.0 ± 0.36	0.658	0.1	2.5 ± 0.18	2.6 ± 0.11
20:4n6	0.011	1.9	6.0 ± 0.56	4.1 ± 0.32			NA	NA
22:5n6	0.314	0.2	1.4 ± 0.19	1.2 ± 0.06	0.002	0.2	1.4 ± 0.02	1.6 ± 0.05
18:3n3	< 0.001	1.6	1.7 ± 0.12	3.3 ± 0.20			NA	NA
20:5n3	0.016	2.1	5.0 ± 0.66	2.9 ± 0.40			NA	NA
22:5n3	0.026	0.8	2.1 ± 0.32	1.3 ± 0.05	0.017	0.3	0.9 ± 0.06	1.2 ± 0.08
22:6n3	0.005	4.1	10.3 ± 1.22	6.2 ± 0.37	0.435	0.7	16.8 ± 0.63	17.5 ± 0.58
others	< 0.001	2.3	3.9 ± 0.17	6.2 ± 0.15	0.837	0.6	35.8 ± 2.29	36.4 ± 1.92
SFA	0.015	4.2	20.2 ± 1.51	16.0 ± 0.51	0.187	1.8	22.0 ± 0.90	20.2 ± 0.86
MUFA	0.002	7.2	43.6 ± 1.73	50.8 ± 0.65	0.934	0.1	20.6 ± 1.24	20.5 ± 1.15
PUFA	0.098	5.3	32.3 ± 2.98	27.0 ± 0.83	0.126	1.3	21.6 ± 0.62	22.9 ± 0.49
all n-6	0.822	0.2	13.2 ± 0.87	13.4 ± 0.36	0.183	0.3	3.9 ± 0.18	4.2 ± 0.12
all n-3	0.024	5.4	19.1 ± 2.13	13.7 ± 0.63	0.278	1.0	17.7 ± 0.65	18.7 ± 0.56
FA conc. % wet wt	< 0.001	1.53	2.0 ± 0.23	0.47 ± 0.055	0.187	0.0	0.03 ± 0.001	0.03 ± 0.001

a - fatty acid compositions are the weight % of the indicated fatty acids in tissue neutral lipids

b - indicates the absolute value of the difference in the indicated variable between warm and cold acclimated pike

c - results of t-test (for unbalanced designs) for significance of differences between warm and cold acclimated pike

Table VI-2. Effect of acclimation temperature on the fatty acid composition of polar lipids in pike white muscle and liver. Data are given as mean ± SE.

Fatty Acid	Liver				Muscle			
	p value^c	$\lvert A-B \rvert^b$	21°C (A) (n=6)	6°C (B) (n=7)	p value^c	$\lvert C-D \rvert^b$	21°C (C) (n=6)	6°C (D) (n=7)
14:0	0.066	0.1	0.7 ± 0.07^a	0.6 ± 0.02	0.007	0.1	0.5 ± 0.02	0.4 ± 0.02
16:0	0.003	3.7	19.7 ± 1.02	16.0 ± 0.21	0.066	0.9	17.6 ± 0.38	16.7 ± 0.25
18:0	0.205	0.2	8.1 ± 0.19	7.9 ± 0.06	< 0.001	0.8	7.5 ± 0.05	6.7 ± 0.08
16:1n7	< 0.001	1.9	5.5 ± 0.11	7.4 ± 0.14	0.004	0.4	3.7 ± 0.10	4.1 ± 0.08
18:1n9	0.127	0.6	12.3 ± 0.35	12.9 ± 0.14	0.067	0.6	10.1 ± 0.23	9.5 ± 0.21
18:2n6	0.065	0.2	1.8 ± 0.06	2.0 ± 0.09	0.002	0.3	1.8 ± 0.06	2.1 ± 0.07
20:4n6	0.094	1.1	9.8 ± 0.56	8.7 ± 0.28	< 0.001	1.5	7.6 ± 0.15	6.1 ± 0.10
22:5n6	0.647	0.1	2.4 ± 0.13	2.3 ± 0.10	0.343	0.1	2.0 ± 0.10	1.9 ± 0.05
18:3n3			NA	NA	< 0.001	0.6	1.5 ± 0.05	2.1 ± 0.06
20:5n3	0.008	0.9	4.5 ± 0.24	5.4 ± 0.19	0.776	0.1	7.2 ± 0.20	7.1 ± 0.14
22:5n3	< 0.001	0.5	1.3 ± 0.06	1.8 ± 0.06	0.050	0.1	2.1 ± 0.07	2.2 ± 0.06
22:6n3	0.110	0.9	32.6 ± 0.46	33.5 ± 0.29	0.014	2.6	34.9 ± 0.56	37.5 ± 0.64
others	0.685	0.0	1.4 ± 0.09	1.4 ± 0.05	0.941	0.0	3.5 ± 0.11	3.5 ± 0.06
SFA	0.001	4.0	28.5 ± 0.97	24.5 ± 0.27	0.004	1.9	25.7 ± 0.40	23.8 ± 0.34
MUFA	< 0.001	2.5	17.8 ± 0.30	20.3 ± 0.21	0.655	0.2	13.9 ± 0.32	13.7 ± 0.28
PUFA	0.162	1.4	52.4 ± 1.02	53.8 ± 0.23	0.034	2.0	57.0 ± 0.64	59.0 ± 0.56
all n-6	0.185	0.9	14.0 ± 0.60	13.1 ± 0.35	< 0.001	1.3	11.4 ± 0.20	10.1 ± 0.17
all n-3	0.003	2.4	38.4 ± 0.56	40.8 ± 0.32	0.006	3.3	45.6 ± 0.64	48.9 ± 0.71
FA conc. % wet wt	0.195	0.1	1.6 ± 0.06	1.5 ± 0.05	< 0.001	0.07	0.38 ± 0.006	0.45 ± 0.008

a - fatty acid compositions are the weight % of the indicated fatty acids in tissue polar lipids

b - indicates the absolute value of the difference in the indicated variable between warm and cold acclimated pike

c - results of t-test (for unbalanced designs) for significance of differences between warm and cold acclimated pike

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Chapter VII

General Discussion

This thesis provides the most thorough examination of the timing and adaptive significance of seasonal fatty acid cycles yet available for any north-temperate freshwater fish species. The major experimental findings from the thesis are summarized in Fig. VII-1, and will be briefly reviewed. Vitellogenesis in pike begins in August (Fig. II-1a), and by the following March the maturing ovaries contain 6.5 g of fatty acids per kg carcass weight (Fig. II-3a,b) which represents a large portion of whole body fatty acid content because the major somatic lipid depots contain only about 10 g of fatty acids per kg carcass weight (Fig. II-4e). The liver weight of pike doubles from August to January (Fig. II-1b) and may be a response to both cold acclimation (chapter VI) and to hormonal changes accompanying ovarian recrudescence (Ng and Idler 1983). Quantities of NLFAs in the liver decline greatly during early winter (Fig. II-3c), possibly due to reductions in food intake (chapter VI), while the content of PLFAs in the liver increases (Fig. II-3d), as a result of greater liver weight and probably also due to a proliferation of membrane bound organelles in association with vitellogenesis (Ng et al. 1984; Mommsen and Walsh 1988). The significant increase in muscle PLFA content during late summer (Fig. II-2h) appears to be a response to cold acclimation (chapter VI) but begins well in advance of declining water temperature. Fatty acids required for ovary growth appear to originate directly from food eaten during winter because the major somatic NLFA depots, muscle and AP tissue, are not significantly depleted during ovarian recrudescence, at least not before March (Figs. II-2g,3e; Table III-8).

The dominant seasonal changes in tissue fatty acid composition of Lac Ste. Anne pike are also shown in Fig. VII-1. Seasonal changes in fatty acid composition which, on the bases of chapters IV and VI, appear to be associated with ovarian recrudescence and temperature acclimation are indicated as such in Fig. VII-1. Ovarian recrudescence in arctic pike appeared to produce reciprocal changes in the percentage of MUFAs and n-3 PUFAs in NLs of both muscle and AP tissue (Fig. IV-1), similar to the changes which occur during fall in Lac Ste. Anne (Fig. III-5). However, question marks beside these responses in Fig. VII-1 indicate there is some uncertainty about whether these changes are real features of ovarian recrudescence because changes in the percentage of MUFAs and n-3 PUFAs of muscle and AP tissue NLs of arctic pike were not statistically significant (Fig. IV-1). Similarly, cold acclimation appeared to produce reciprocal changes in the percentage of MUFAs and n-3 PUFAs in liver NLs, but only the change in MUFAs was significant (Fig. VI-2).

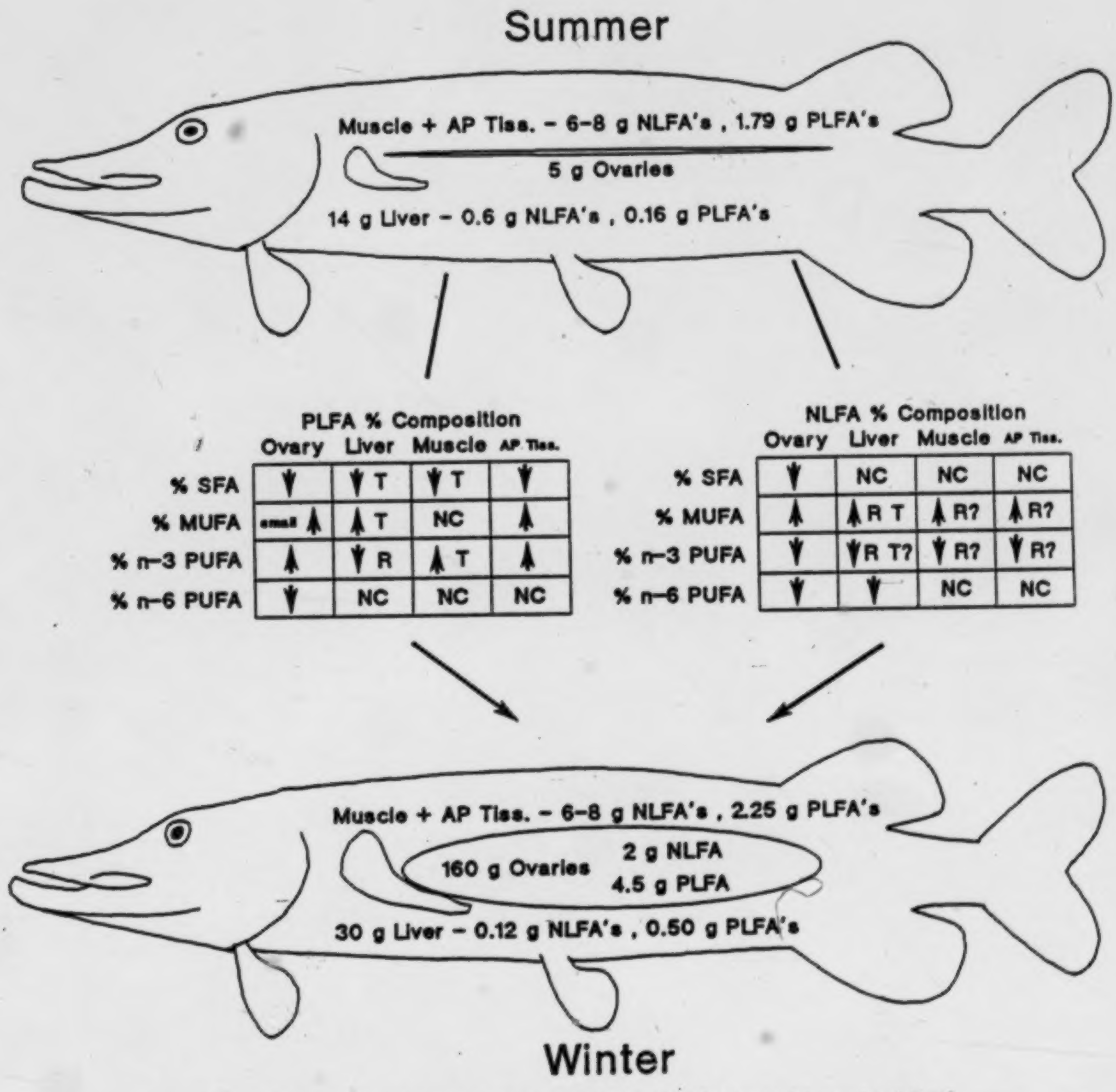
This work makes several important contributions to our knowledge of the seasonal effects of environmental factors on fish fatty acid composition. First, the data presented indicate that several environmental and physiological factors contribute to seasonal fatty acid cycles in pike. Therefore, laboratory experiments designed to identify the influence of a single factor (eg: diet or temperature) on fatty acid metabolism may not indicate accurately or completely the effects this factor has in wild fish populations. Temperature acclimation is perhaps the best factor to illustrate this. Cold acclimation in pike produced significant declines in the percentage of SFAs in liver NLs and increases in the percentage of n-3 PUFAs in liver PLs (Fig. VI-2). Other studies have reported an increase in the percentage of n-3 and n-6 PUFAs in liver NLs of fish during cold acclimation (Hazel 1979). However, none of these changes accompany winter acclimatization in wild pike (Fig. III-4).

Even when temperature acclimation produces responses similar to those observed in wild fish, such responses must be interpreted with caution. For example, winter acclimatization in wild pike (Figs. II-1,3, III-4) and cold acclimation under laboratory conditions (Figs. VI-1,2) were both associated with increases in liver weight, liver PLFA content, and reciprocal changes in the percentages of MUFAs and n-3 PUFAs in liver NLs. However, the changes observed in wild pike may not be solely, or even predominantly, responses to temperature because ovarian recrudescence may also increase liver weight, liver PLFA content, and produce reciprocal changes in the percentages of MUFAs and n-3 PUFAs in liver NLs (Table IV-1, Fig. IV-1).

Laboratory studies on the effects of temperature on fish fatty acid metabolism generally do not consider how the physiological responses elicited by temperature change might be modified in wild fish by the effects of ovarian recrudescence, and changes in food intake and diet composition (Hazel 1979a,b, 1990). This thesis suggests that studies of environmental influences on fish fatty acid metabolism will be more valuable if they include data from natural populations as a reference for assessing the adaptive significance of laboratory findings.

Data presented in this thesis also suggest that the availability of EFAs, especially the n-3 PUFAs, may impose certain physiological restrictions on fish. The reason fish and other animals do not synthesize n-3 or n-6 EFAs is presumably because the diet normally provides sufficient quantities of these compounds. Chapter V showed that the relative proportions of the various long chain EFAs in pike lipids were approximately the same as in dietary lipids. This suggests that pike, like other strict carnivores (Owen et al. 1975; Davidson et al. 1990), may not chain elongate and further desaturate dietary EFAs to any great extent. Such a strategy saves the animal the expense of synthesizing enzymes and expending energy to interconvert dietary fatty acids. However, the animal may experience physiological consequences if its dietary intake of EFAs should decline for any reason.

It was earlier hypothesized that during winter north-temperate fish may experience physiological consequences related to EFA availability due to the combined effects of reduced EFA intake and increased EFA requirements for ovary growth and PL restructuring. Pike in Lac Ste. Anne obviously do not experience significant EFA deficiency over winter because they are able to maintain levels of EFAs in PLs and otherwise appear to thrive in this environment. However, the percentage of n-3 PUFAs declines significantly over winter in the NLs of all four tissues examined (Figs. III-4,5). The most plausible explanation for this phenomenon is that it conserves dietary EFAs for incorporation into tissue PLs, wherein the content of n-3 PUFAs increases significantly over winter (Table III-8). Therefore, a reduced dietary availability of n-3 PUFAs over winter may have exerted selection pressure on pike in the past and initiated the evolution of mechanisms to conserve n-3 PUFAs in these fish. For these reasons, it is worthwhile to look for more serious physiological consequences related to EFA availability in fish populations inhabiting more extreme environments such as those at the boundaries of a species geographic range and in fish populations feeding on unusual foods (Chapman and Mackay 1990).


Summer
Muscle + AP Tiss. - 6-8 g NLFA's , 1.79 g PLFA's
5 g Ovaries
14 g Liver - 0.6 g NLFA's , 0.16 g PLFA's
Muscle + AP Tiss. - 6-8 g NLFA's , 2.25 g PLFA's
160 g Ovaries
2 g NLFA
4.5 g PLFA
30 g Liver - 0.12 g NLFA's , 0.50 g PLFA's
Winter

PLFA % Composition

	Ovary	Liver	Muscle	AP Tiss.
% SFA	↓	↓ T	↓ T	↓
% MUFA	small ↑	↑ T	NC	↑
% n-3 PUFA	↑	↓ R	↑ T	↑
% n-6 PUFA	↓	NC	NC	NC

NLFA % Composition

	Ovary	Liver	Muscle	AP Tiss.
% SFA	↓	NC	NC	NC
% MUFA	↑	↑ R T	↑ R?	↑ R?
% n-3 PUFA	↓	↓ R T?	↓ R?	↓ R?
% n-6 PUFA	↓	↓	NC	NC

Figure VII-1. Summary of seasonal changes in the fatty acid content and composition of female pike. Quantities of NLFA's and PLFA's in tissues of a 1 kg carcass wt pike are indicated inside the pike outlines. Changes in fatty acid composition from summer to winter are indicated in the centre. Letters R and T indicate whether the change appears to be associated with ovarian recrudescence, temperature, or both. NC means no change.

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Appendices

Footnotes to appendices 1 to 10.

a - fatty acid composition is expressed as the mean weight % of the indicated fatty acids in tissue lipids.

b - sample sizes are given directly below each sampling date.

c - p values show the statistical significance of seasonal variation for each variable as tested using one-way ANOVA.

d - seasonal range refers to the difference between the highest and lowest monthly mean recorded for that variable over the fifteen month sampling period.

e - data for pike which had not spawned and still contained mature eggs.

f - data for pike which had spawned all their eggs.

Appendix 1. Seasonal changes in the fatty acid composition of neutral lipids from pike tissues. Mean ± SE

			Ovary									
			1987					1988				
Fatty Acid	p Value[c]	Seasonal[d] Range wt %	May	June[b] 6	July 6	August 7	Sept. 7	Jan. 7	March 7	May[e] 3	May[f] 4	June 8	Aug.
16:0	<0.001	6.6	-----	15.1[a] ± 0.39	16.5 ± 0.07	14.6 ± 0.37	13.2 ± 0.69	9.9 ± 0.14	9.9 ± 0.14	10.3 ± 0.14	12.6 ± 0.57	15.6 ± 0.83	-----
18:0	<0.001	2.9	-----	7.2 ± 0.26	7.1 ± 0.19	4.7 ± 0.13	5.7 ± 0.42	6.9 ± 0.11	6.9 ± 0.13	6.6 ± 0.08	6.0 ± 0.30	7.6 ± 0.38	-----
16:1n7	<0.001	5.1	-----	13.3 ± 0.35	14.4 ± 0.17	14.6 ± 0.24	14.1 ± 0.39	17.5 ± 0.27	18.4 ± 0.21	18.2 ± 0.27	15.8 ± 0.71	16.0 ± 0.44	-----
18:1n9	<0.001	16.0	-----	18.7 ± 0.68	18.0 ± 0.43	16.6 ± 0.22	21.6 ± 1.54	32.6 ± 0.56	31.2 ± 0.44	29.8 ± 0.26	21.9 ± 1.36	19.1 ± 0.76	-----
18:2n6	<0.001	1.6	-----	5.3 ± 0.07	5.4 ± 0.08	4.8 ± 0.12	5.7 ± 0.19	6.4 ± 0.09	6.2 ± 0.11	6.2 ± 0.24	4.8 ± 0.19	4.8 ± 0.13	-----
20:4n6	<0.001	3.3	-----	6.2 ± 0.33	5.9 ± 0.23	5.4 ± 0.23	5.2 ± 0.16	2.9 ± 0.13	3.0 ± 0.06	3.4 ± 0.26	5.8 ± 0.51	5.3 ± 0.20	-----
22:5n6	<0.001	0.79	-----	1.51 ± 0.14	1.43 ± 0.04	1.54 ± 0.07	1.35 ± 0.09	0.76 ± 0.03	0.79 ± 0.02	0.79 ± 0.05	1.55 ± 0.18	1.49 ± 0.05	-----
18:3n3	0.008	1.4	-----	3.4 ± 0.20	4.1 ± 0.18	4.0 ± 0.28	4.0 ± 0.27	4.2 ± 0.13	4.3 ± 0.15	4.7 ± 0.31	3.8 ± 0.25	3.3 ± 0.15	-----
20:5n3	<0.001	4.0	-----	6.9 ± 0.33	6.8 ± 0.51	7.0 ± 0.36	6.1 ± 0.31	3.0 ± 0.11	3.3 ± 0.15	3.7 ± 0.05	6.3 ± 0.45	6.7 ± 0.19	-----
22:5n3	<0.001	0.9	-----	2.1 ± 0.04	1.9 ± 0.06	1.9 ± 0.13	1.6 ± 0.15	1.2 ± 0.03	1.2 ± 0.05	1.3 ± 0.09	2.0 ± 0.11	2.1 ± 0.08	-----
22:6n3	<0.001	10.8	-----	15.0 ± 0.58	14.4 ± 0.45	22.0 ± 0.54	18.5 ± 1.56	11.3 ± 0.39	11.2 ± 0.28	11.6 ± 0.64	16.0 ± 1.75	14.5 ± 0.65	-----
others	<0.001	2.6	-----	5.3 ± 0.49	4.0 ± 0.13	2.8 ± 0.11	2.7 ± 0.11	3.5 ± 0.14	3.5 ± 0.07	3.5 ± 0.13	3.5 ± 0.16	3.4 ± 0.15	-----
SFA	<0.001	6.9	-----	22.3 ± 0.49	23.6 ± 0.23	19.3 ± 0.48	18.9 ± 0.80	16.7 ± 0.22	16.8 ± 0.23	16.9 ± 0.22	18.6 ± 0.81	23.2 ± 1.19	-----
MUFA	<0.001	18.9	-----	32.0 ± 0.91	32.5 ± 0.39	31.2 ± 0.42	35.8 ± 1.53	50.1 ± 0.63	49.6 ± 0.43	48.0 ± 0.19	37.7 ± 1.90	35.2 ± 1.03	-----
PUFA	<0.001	16.9	-----	40.4 ± 1.08	39.9 ± 0.54	46.6 ± 0.83	42.6 ± 1.74	29.7 ± 0.67	30.1 ± 0.51	31.6 ± 0.49	40.2 ± 2.49	38.2 ± 0.86	-----
all n-6	<0.001	3.0	-----	13.0 ± 0.37	12.7 ± 0.24	11.8 ± 0.21	12.3 ± 0.29	10.1 ± 0.15	10.0 ± 0.11	10.3 ± 0.38	12.1 ± 0.62	11.5 ± 0.26	-----
all n-3	<0.001	15.3	-----	27.3 ± 0.75	27.2 ± 0.45	34.9 ± 0.77	30.3 ± 1.75	19.6 ± 0.61	20.0 ± 0.41	21.3 ± 0.57	28.1 ± 1.90	26.7 ± 0.74	-----
c-16	<0.001	4.3	-----	28.5 ± 0.69	31.0 ± 0.16	29.2 ± 0.55	27.4 ± 0.67	27.4 ± 0.35	28.3 ± 0.16	28.5 ± 0.24	28.4 ± 1.22	31.7 ± 0.65	-----
c-18	<0.001	19.9	-----	34.6 ± 0.76	34.6 ± 0.61	30.2 ± 0.42	37.0 ± 2.18	50.1 ± 0.52	48.7 ± 0.42	47.3 ± 0.58	36.5 ± 1.82	34.8 ± 0.65	-----
c-20	<0.001	7.2	-----	13.1 ± 0.48	12.7 ± 0.58	12.4 ± 0.48	11.4 ± 0.40	5.9 ± 0.22	6.3 ± 0.18	7.0 ± 0.31	12.1 ± 0.59	12.0 ± 0.28	-----
c-22	<0.001	12.2	-----	18.6 ± 0.71	17.7 ± 0.46	25.4 ± 0.56	21.5 ± 1.73	13.2 ± 0.43	13.3 ± 0.34	13.7 ± 0.65	19.5 ± 1.93	18.1 ± 0.72	-----

Appendix 1. cont... Seasonal changes in the fatty acid composition of neutral lipids from pike tissues.

			Liver									
		Seasonal[d]	1987					1988				
Fatty Acid	p Value[c]	Range wt %	May	June[b] 7	July 6	August 7	Sept. 5	Jan. 7	March 7	May 7	June 8	Aug. 6
16:0	<0.001	4.6	-----	14.8[a] ± 1.34	11.3 ± 0.73	10.2 ± 0.31	10.7 ± 0.27	11.2 ± 0.30	11.0 ± 0.36	13.6 ± 0.93	11.3 ± 0.76	11.0 ± 0.62
18:0	<0.001	1.7	-----	6.4 ± 0.27	6.5 ± 0.27	6.7 ± 0.22	7.7 ± 0.28	7.3 ± 0.20	7.4 ± 0.24	6.3 ± 0.28	6.0 ± 0.23	6.3 ± 0.35
16:1n7	<0.001	7.7	-----	14.7 ± 0.40	12.9 ± 0.38	14.2 ± 0.30	16.0 ± 0.36	19.2 ± 0.15	20.6 ± 0.33	18.6 ± 0.71	15.2 ± 0.54	14.8 ± 0.38
18:1n9	0.068	6.3	-----	29.5 ± 2.55	25.1 ± 1.36	25.6 ± 0.61	31.4 ± 1.19	31.3 ± 1.19	30.1 ± 1.92	28.6 ± 1.77	27.9 ± 1.68	26.5 ± 0.93
18:2n6	<0.001	3.5	-----	5.5 ± 0.63	7.4 ± 0.48	8.9 ± 0.21	9.0 ± 0.23	6.8 ± 0.24	7.0 ± 0.24	6.6 ± 0.70	6.3 ± 0.46	8.3 ± 0.44
20:4n6	<0.001	2.2	-----	4.5 ± 0.36	4.8 ± 0.13	4.5 ± 0.22	4.4 ± 0.27	3.1 ± 0.15	3.5 ± 0.30	4.1 ± 0.21	5.2 ± 0.16	5.3 ± 0.41
22:5n6	0.001	0.42	-----	0.74 ± 0.11	1.13 ± 0.09	1.11 ± 0.04	0.86 ± 0.07	0.80 ± 0.08	0.80 ± 0.10	0.93 ± 0.12	1.14 ± 0.08	1.16 ± 0.06
18:3n3	<0.001	3.1	-----	3.2 ± 0.53	4.8 ± 0.46	6.3 ± 0.51	5.3 ± 0.40	4.9 ± 0.30	5.3 ± 0.38	4.5 ± 0.47	3.7 ± 0.35	3.8 ± 0.17
20:5n3	<0.001	3.4	-----	6.3 ± 0.93	6.7 ± 0.39	5.3 ± 0.37	3.9 ± 0.67	3.3 ± 0.11	3.5 ± 0.40	4.1 ± 0.33	6.4 ± 0.50	6.6 ± 0.66
22:5n3	<0.001	1.8	-----	2.0 ± 0.23	2.6 ± 0.10	1.9 ± 0.14	1.1 ± 0.17	1.0 ± 0.03	0.9 ± 0.13	1.1 ± 0.15	2.3 ± 0.20	2.7 ± 0.14
22:6n3	<0.001	6.7	-----	8.7 ± 1.08	12.6 ± 0.93	10.4 ± 0.70	6.0 ± 0.68	7.0 ± 0.49	5.9 ± 0.87	7.8 ± 0.92	10.5 ± 0.66	9.7 ± 1.11
others	0.004	1.4	-----	3.9 ± 0.35	4.1 ± 0.21	5.0 ± 0.36	3.6 ± 0.25	4.1 ± 0.14	3.9 ± 0.10	3.7 ± 0.19	4.1 ± 0.11	3.9 ± 0.19
SFA	0.012	4.5	-----	21.3 ± 1.43	17.8 ± 0.92	16.8 ± 0.45	18.4 ± 0.50	18,5 ± 0.43	18.4 ± 0.36	19.9 ± 0.94	17.3 ± 0.95	17.3 ± 0.95
MUFA	<0.001	12.8	-----	44.2 ± 2.67	38.0 ± 1.42	39.7 ± 0.55	47.5 ± 1.44	50.5 ± 1.18	50.8 ± 2.11	47.2 ± 2.09	43.1 ± 1.70	41.3 ± 1.07
PUFA	<0.001	13.2	-----	30.7 ± 3.74	40.1 ± 2.04	38.4 ± 0.72	30.6 ± 1.63	26.9 ± 0.84	26.9 ± 2.05	29.2 ± 2.58	35.5 ± 2.17	37.5 ± 1.88
all n-6	<0.001	4.2	-----	10.5 ± 1.08	13.4 ± 0.56	14.5 ± 0.21	14.3 ± 0.32	10.8 ± 0.31	11.3 ± 0.57	11.6 ± 0.97	12.6 ± 0.60	14.7 ± 0.21
all n-3	<0.001	11.1	-----	20.2 ± 2.71	26.7 ± 1.56	23.8 ± 0.69	16.3 ± 1.38	16.1 ± 0.64	15.6 ± 1.54	17.6 ± 1.70	22.9 ± 1.61	22.8 ± 1.76
c-16	<0.001	8.0	-----	29.5 ± 1.58	24.2 ± 0.89	24.3 ± 0.52	26.7 ± 0.58	30.4 ± 0.37	31.6 ± 0.33	32.2 ± 1.35	26.5 ± 0.57	25.7 ± 0.83
c-18	<0.001	9.7	-----	44.3 ± 1.59	43.9 ± 0.95	47.4 ± 0.92	53.5 ± 1.28	50.4 ± 1.04	49.8 ± 1.72	46.0 ± 1.05	43.8 ± 1.03	45.0 ± 1.38
c-20	<0.001	5.5	-----	10.9 ± 1.27	11.5 ± 0.45	9.9 ± 0.54	8.3 ± 0.88	6.4 ± 0.25	7.0 ± 0.69	8.2 ± 0.50	11.6 ± 0.60	11.9 ± 1.04
c-22	<0.001	8.7	-----	11.4 ± 1.37	16.3 ± 1.06	13.4 ± 0.85	8.0 ± 0.86	8.8 ± 0.59	7.6 ± 1.09	9.9 ± 1.18	14.0 ± 0.91	13.5 ± 1.23

Appendix 1. cont... Seasonal changes in the fatty acid composition of neutral lipids from pike tissues.

			Muscle									
		Seasonal[d]	1987					1988				
Fatty Acid	p Value[c]	Range wt %	May[b] 5	June 6	July 6	August 7	Sept. 6	Jan. 6	March 7	May 7	June 7	Aug. 6
16:0	0.019	2.0	13.2[a]	14.8	14.5	13.5	13.2	13.4	12.8	12.9	13.6	13.4
			± 0.31	± 0.85	± 0.37	± 0.36	± 0.29	± 0.37	± 0.26	± 0.19	± 0.33	± 0.39
18:0	0.014	0.6	6.3	6.4	6.4	5.8	6.3	6.2	6.2	6.0	6.4	6.1
			± 0.21	± 0.16	± 0.07	± 0.11	± 0.19	± 0.08	± 0.08	± 0.07	± 0.16	± 0.12
16:1n7	<0.001	5.3	16.2	13.8	14.5	15.3	15.5	17.1	18.7	19.1	17.8	17.9
			± 0.58	± 0.49	± 0.35	± 0.19	± 0.28	± 0.52	± 0.38	± 0.26	± 0.26	± 0.23
18:1n9	0.026	2.3	19.6	18.3	17.9	18.2	18.1	19.2	20.2	19.6	20.1	18.4
			± 0.47	± 0.91	± 0.79	± 0.44	± 0.33	± 0.42	± 0.46	± 0.33	± 0.83	± 0.41
18:2n6	0.162	0.8	6.1	5.9	5.8	6.3	6.5	6.2	6.0	6.2	5.8	6.6
			± 0.32	± 0.17	± 0.10	± 0.16	± 0.17	± 0.13	± 0.23	± 0.31	± 0.26	± 0.19
20:4n6	0.002	1.0	4.3	5.1	4.5	4.3	4.2	4.2	4.1	4.3	4.4	4.4
			± 0.12	± 0.33	± 0.10	± 0.08	± 0.10	± 0.09	± 0.06	± 0.17	± 0.07	± 0.13
22:5n6	0.238	0.2	1.1	1.3	1.3	1.2	1.3	1.1	1.1	1.1	1.1	1.3
			± 0.07	± 0.18	± 0.08	± 0.06	± 0.07	± 0.04	± 0.04	± 0.05	± 0.06	± 0.06
18:3n3	<0.001	1.3	6.3	5.9	5.8	6.7	6.5	6.8	7.0	6.6	5.7	5.7
			± 0.21	± 0.19	± 0.17	± 0.29	± 0.23	± 0.12	± 0.22	± 0.12	± 0.25	± 0.15
20:5n3	0.242	1.0	6.0	6.6	6.6	6.3	5.6	6.0	6.5	6.6	6.2	6.3
			± 0.39	± 0.19	± 0.32	± 0.35	± 0.22	± 0.19	± 0.24	± 0.24	± 0.33	± 0.11
22:5n3	<0.001	0.5	1.5	1.8	1.9	1.9	2.0	1.6	1.5	1.5	1.8	2.0
			± 0.08	± 0.05	± 0.08	± 0.04	± 0.03	± 0.05	± 0.06	± 0.07	± 0.08	± 0.04
22:6n3	<0.001	4.6	10.9	10.4	12.5	12.3	12.7	9.6	8.1	8.4	9.8	10.7
			± 0.34	± 0.75	± 0.30	± 0.48	± 0.37	± 0.30	± 0.34	± 0.33	± 0.35	± 0.47
others	0.002	2.8	8.5	9.8	8.4	8.2	8.1	8.4	7.7	7.9	7.2	7.0
			± 0.14	± 0.90	± 0.35	± 0.41	± 0.24	± 0.18	± 0.20	± 0.26	± 0.46	± 0.27
SFA	0.020	2.3	19.4	21.2	20.9	19.3	19.5	19.7	19.0	18.9	20.0	19.5
			± 0.51	± 0.97	± 0.41	± 0.46	± 0.46	± 0.45	± 0.32	± 0.23	± 0.43	± 0.48
MUFA	<0.001	6.8	35.8	32.1	32.3	33.5	33.6	36.4	38.9	38.7	37.9	36.4
			± 0.45	± 1.14	± 0.54	± 0.47	± 0.39	± 0.44	± 0.23	± 0.28	± 0.77	± 0.47
PUFA	<0.001	4.5	36.2	36.9	38.4	38.9	38.8	35.5	34.4	34.6	34.9	37.1
			± 0.72	± 1.21	± 0.50	± 1.06	± 0.36	± 0.64	± 0.38	± 0.36	± 0.58	± 0.56
all n-6	0.132	1.1	11.5	12.3	11.6	11.8	12.0	11.5	11.2	11.6	11.3	12.3
			± 0.45	± 0.51	± 0.15	± 0.15	± 0.15	± 0.17	± 0.23	± 0.47	± 0.24	± 0.12
all n-3	<0.001	4.1	24.7	24.6	26.8	27.1	26.8	24.0	23.1	23.0	23.5	24.8
			± 0.36	± 0.80	± 0.41	± 0.94	± 0.26	± 0.54	± 0.38	± 0.27	± 0.55	± 0.53
c-16	<0.001	3.4	29.4	28.6	28.9	28.8	28.8	30.6	31.5	32.0	31.4	31.3
			± 0.60	± 1.03	± 0.41	± 0.34	± 0.14	± 0.57	± 0.16	± 0.36	± 0.23	± 0.44
c-18	<0.001	3.5	38.2	36.5	35.9	36.9	37.4	38.5	39.4	38.3	38.0	36.9
			± 0.36	± 0.82	± 0.59	± 0.24	± 0.41	± 0.33	± 0.62	± 0.31	± 0.45	± 0.56
c-20	0.036	1.8	10.3	11.6	11.1	10.6	9.8	10.1	10.6	10.9	10.6	10.8
			± 0.38	± 0.38	± 0.34	± 0.38	± 0.30	± 0.25	± 0.29	± 0.32	± 0.36	± 0.22
c-22	<0.001	5.2	13.6	13.5	15.7	15.4	15.9	12.4	10.7	10.9	12.8	14.0
			± 0.48	± 0.89	± 0.34	± 0.56	± 0.44	± 0.37	± 0.40	± 0.40	± 0.41	± 0.56

Appendix 1. cont... Seasonal changes in the fatty acid composition of neutral lipids from pike tissues.

			Adipopancreatic tissue									
		Seasonal[d]	1987					1988				
Fatty Acid	p value[c]	Range wt %	May[b] 5	June 7	July 6	August 7	Sept. 7	Jan. 7	March 7	May 7	June 8	Aug. 6
16:0	<0.001	3.1	13.1[a] ± 0.44	15.1 ± 0.77	13.5 ± 0.35	12.9 ± 0.21	12.9 ± 0.31	12.6 ± 0.28	12.0 ± 0.36	12.2 ± 0.14	12.9 ± 0.17	13.1 ± 0.36
18:0	0.001	0.6	6.0 ± 0.16	6.1 ± 0.20	5.8 ± 0.08	5.5 ± 0.07	6.0 ± 0.14	5.8 ± 0.08	5.5 ± 0.09	5.5 ± 0.07	5.7 ± 0.10	5.7 ± 0.11
16:1n7	<0.001	5.2	18.0 ± 0.52	15.2 ± 0.33	15.4 ± 0.22	16.2 ± 0.18	16.0 ± 0.27	18.9 ± 0.28	20.3 ± 0.42	20.4 ± 0.23	18.5 ± 0.31	18.9 ± 0.27
18:1n9	0.142	2.5	20.1 ± 0.90	19.7 ± 1.00	18.3 ± 1.15	17.8 ± 0.35	18.3 ± 0.39	19.4 ± 0.31	18.6 ± 0.49	19.0 ± 0.44	20.3 ± 0.76	18.8 ± 0.41
18:2n6	0.163	0.9	6.6 ± 0.52	6.1 ± 0.15	6.3 ± 0.25	6.8 ± 0.21	6.7 ± 0.15	6.7 ± 0.17	6.5 ± 0.20	6.8 ± 0.29	6.1 ± 0.29	7.0 ± 0.28
20:4n6	0.149	0.5	3.9 ± 0.27	4.4 ± 0.07	4.3 ± 0.15	4.0 ± 0.13	4.2 ± 0.16	4.0 ± 0.11	4.0 ± 0.07	4.3 ± 0.12	4.2 ± 0.08	4.1 ± 0.15
22:5n6	0.027	0.38	0.99 ± 0.09	1.04 ± 0.08	1.37 ± 0.10	1.19 ± 0.06	1.26 ± 0.08	1.08 ± 0.06	1.06 ± 0.06	1.14 ± 0.06	1.14 ± 0.07	1.25 ± 0.06
18:3n3	<0.001	1.9	6.7 ± 0.31	6.0 ± 0.23	6.4 ± 0.28	7.8 ± 0.47	6.8 ± 0.29	7.6 ± 0.33	7.6 ± 0.22	7.2 ± 0.14	6.1 ± 0.24	5.9 ± 0.12
20:5n3	0.102	1.2	5.9 ± 0.37	6.8 ± 0.29	6.1 ± 0.29	6.0 ± 0.32	5.6 ± 0.14	5.8 ± 0.10	6.2 ± 0.14	5.8 ± 0.38	6.2 ± 0.22	5.8 ± 0.21
22:5n3	<0.001	0.8	1.4 ± 0.04	1.9 ± 0.12	2.1 ± 0.06	1.9 ± 0.10	2.2 ± 0.11	1.6 ± 0.10	1.6 ± 0.08	1.4 ± 0.06	2.0 ± 0.09	2.0 ± 0.05
22:6n3	<0.001	5.2	9.4 ± 1.00	10.2 ± 0.90	12.9 ± 0.69	11.9 ± 0.49	12.3 ± 0.52	8.9 ± 0.48	8.4 ± 0.45	7.7 ± 0.45	9.7 ± 0.39	10.3 ± 0.55
others	0.007	1.5	7.9 ± 0.45	7.6 ± 0.40	7.7 ± 0.30	8.0 ± 0.20	7.7 ± 0.25	7.7 ± 0.16	8.3 ± 0.28	8.6 ± 0.22	7.1 ± 0.30	7.1 ± 0.24
SFA	<0.001	3.6	19.1 ± 0.60	21.1 ± 0.95	19.3 ± 0.40	18.4 ± 0.23	19.0 ± 0.42	18.4 ± 0.34	17.5 ± 0.44	17.6 ± 0.18	18.7 ± 0.17	18.8 ± 0.45
MUFA	<0.001	5.7	38.1 ± 1.03	34.8 ± 0.76	33.7 ± 1.09	34.0 ± 0.43	34.2 ± 0.32	38.3 ± 0.25	38.8 ± 0.28	39.4 ± 0.38	38.8 ± 0.65	37.7 ± 0.39
PUFA	<0.001	5.2	34.9 ± 1.25	36.5 ± 1.15	39.3 ± 1.04	39.6 ± 0.32	39.1 ± 0.45	35.6 ± 0.29	35.3 ± 0.43	34.4 ± 0.24	35.4 ± 0.36	36.3 ± 0.50
all n-6	0.100	1.0	11.5 ± 0.62	11.6 ± 0.21	11.9 ± 0.30	11.9 ± 0.09	12.2 ± 0.14	11.7 ± 0.07	11.6 ± 0.23	12.3 ± 0.36	11.4 ± 0.25	12.4 ± 0.14
all n-3	<0.001	5.5	23.5 ± 1.22	24.9 ± 1.11	27.4 ± 0.78	27.6 ± 0.28	26.9 ± 0.40	23.9 ± 0.31	23.8 ± 0.40	22.1 ± 0.52	24.0 ± 0.28	24.0 ± 0.63
c-16	<0.001	3.6	31.1 ± 0.50	30.2 ± 0.49	28.9 ± 0.25	29.1 ± 0.28	28.9 ± 0.33	31.5 ± 0.22	32.2 ± 0.25	32.5 ± 0.18	31.4 ± 0.22	32.0 ± 0.34
c-18	0.418	2.6	39.4 ± 1.05	37.9 ± 0.98	36.8 ± 0.79	37.9 ± 0.75	37.9 ± 0.64	39.4 ± 0.73	38.2 ± 0.80	38.5 ± 0.67	38.3 ± 0.43	37.4 ± 0.66
c-20	0.100	1.5	9.7 ± 0.52	11.2 ± 0.29	10.3 ± 0.40	9.9 ± 0.43	9.8 ± 0.25	9.8 ± 0.20	10.2 ± 0.19	10.1 ± 0.39	10.4 ± 0.27	9.9 ± 0.33
c-22	<0.001	6.1	11.8 ± 1.06	13.1 ± 1.02	16.3 ± 0.76	15.1 ± 0.61	15.7 ± 0.65	11.6 ± 0.62	11.1 ± 0.57	10.2 ± 0.53	12.8 ± 0.50	13.6 ± 0.65

Appendix 2. Seasonal changes in the fatty acid composition of polar lipids from pike tissues. Mean ± SE

			Ovary										
			1987					1988					
Fatty Acid	p Value[c]	Seasonal[d] Range wt %	May[b]	June	July	August	Sept.	Jan.	March	May[e]	May[f]	June	Aug.
			5	7	6	7	7	7	7	3	4	8	
14:0	<0.001	0.5	1.1[a]	1.4	1.5	1.2	1.0	1.4	1.4	1.5	1.1	1.3	-----
			± 0.09	± 0.07	± 0.04	± 0.05	± 0.05	± 0.03	± 0.02	± 0.01	± 0.08	± 0.04	
16:0	<0.001	3.2	18.4	20.2	21.1	21.1	20.9	19.4	19.3	19.5	17.9	19.4	-----
			± 0.28	± 0.24	± 0.17	± 0.22	± 0.27	± 0.13	± 0.18	± 0.13	± 0.19	± 0.27	
18:0	<0.001	5.9	10.0	10.5	9.3	8.1	6.6	4.7	4.8	4.7	9.2	10.6	-----
			± 0.41	± 0.09	± 0.16	± 0.12	± 0.22	± 0.04	± 0.05	± 0.07	± 0.37	± 0.21	
16:1n7	<0.001	2.6	7.8	7.6	8.1	8.3	8.4	9.9	10.2	10.1	8.7	8.1	-----
			± 0.27	± 0.29	± 0.15	± 0.27	± 0.20	± 0.07	± 0.10	± 0.17	± 0.29	± 0.19	
18:1n9	<0.001	2.5	14.8	13.9	14.3	13.7	12.3	14.0	13.3	12.9	14.6	13.9	-----
			± 0.24	± 0.17	± 0.19	± 0.21	± 0.19	± 0.19	± 0.15	± 0.25	± 0.18	± 0.23	
18:2n6	<0.001	1.3	2.0	1.6	1.8	2.2	2.2	2.8	2.7	2.6	2.2	1.5	-----
			± 0.18	± 0.03	± 0.07	± 0.13	± 0.08	± 0.06	± 0.06	± 0.08	± 0.12	± 0.07	
20:4n6	<0.001	6.9	14.3	13.9	11.3	10.3	9.6	7.7	7.5	7.4	13.5	13.4	-----
			± 0.53	± 0.33	± 0.18	± 0.23	± 0.25	± 0.09	± 0.07	± 0.23	± 0.31	± 0.32	
22:5n6	0.005	0.3	1.5	1.3	1.5	1.4	1.5	1.5	1.5	1.4	1.6	1.6	-----
			± 0.11	± 0.05	± 0.04	± 0.04	± 0.07	± 0.02	± 0.03	± 0.07	± 0.08	± 0.05	
18:3n3	<0.001	1.5	1.5	1.1	1.2	1.5	1.7	2.5	2.5	2.5	1.8	1.0	-----
			± 0.06	± 0.05	± 0.04	± 0.11	± 0.11	± 0.04	± 0.08	± 0.05	± 0.07	± 0.02	
20:5n3	<0.001	2.2	6.5	7.6	7.8	8.4	8.1	7.6	7.3	7.2	6.2	7.6	-----
			± 0.37	± 0.18	± 0.21	± 0.19	± 0.22	± 0.09	± 0.12	± 0.33	± 0.33	± 0.35	
22:5n3	<0.001	0.7	1.9	1.7	1.4	1.4	1.7	1.9	1.9	2.0	2.1	1.7	-----
			± 0.15	± 0.07	± 0.05	± 0.05	± 0.08	± 0.04	± 0.06	± 0.10	± 0.14	± 0.04	
22:6n3	<0.001	9.3	16.6	15.1	16.9	18.9	22.4	22.9	23.8	24.4	17.4	16.1	-----
			± 0.50	± 0.21	± 0.27	± 0.45	± 0.40	± 0.13	± 0.25	± 0.81	± 0.35	± 0.25	
others	<0.001	0.6	3.6	4.0	3.8	3.4	3.5	4.0	3.8	3.8	3.8	3.8	-----
			± 0.26	± 0.05	± 0.05	± 0.07	± 0.05	± 0.11	± 0.12	± 0.17	± 0.08	± 0.07	
SFA	<0.001	6.7	29.6	32.1	31.9	30.4	28.6	25.4	25.5	25.7	28.2	31.2	-----
			± 0.18	± 0.24	± 0.27	± 0.18	± 0.26	± 0.16	± 0.15	± 0.11	± 0.23	± 0.36	
MUFA	<0.001	3.2	22.7	21.5	22.4	22.0	20.7	23.9	23.5	23.0	23.3	22.0	-----
			± 0.07	± 0.20	± 0.22	± 0.32	± 0.19	± 0.20	± 0.15	± 0.14	± 0.28	± 0.15	
PUFA	<0.001	5.6	44.2	42.3	41.9	44.2	47.1	46.7	47.2	47.5	44.8	42.9	-----
			± 0.41	± 0.27	± 0.41	± 0.33	± 0.25	± 0.13	± 0.15	± 0.25	± 0.39	± 0.51	
all n-6	<0.001	6.4	17.8	16.8	14.6	13.9	13.3	12.0	11.6	11.4	17.3	16.5	-----
			± 0.61	± 0.31	± 0.18	± 0.21	± 0.25	± 0.05	± 0.06	± 0.25	± 0.29	± 0.29	
all n-3	<0.001	10.6	26.5	25.5	27.3	30.2	33.9	34.7	35.5	36.1	27.5	26.4	-----
			± 0.74	± 0.26	± 0.33	± 0.44	± 0.38	± 0.10	± 0.20	± 0.48	± 0.58	± 0.52	
c-16	<0.001	3.4	26.3	27.8	29.2	29.4	29.4	29.2	29.4	29.7	26.6	27.5	-----
			± 0.44	± 0.30	± 0.18	± 0.16	± 0.16	± 0.10	± 0.15	± 0.11	± 0.44	± 0.35	
c-18	<0.001	5.6	28.3	27.0	26.6	25.6	22.8	24.0	23.3	22.7	27.8	27.1	-----
			± 0.78	± 0.19	± 0.35	± 0.35	± 0.28	± 0.17	± 0.20	± 0.22	± 0.50	± 0.36	
c-20	<0.001	6.9	20.7	21.5	19.1	18.7	17.7	15.1	14.8	14.6	19.6	20.9	-----
			± 0.44	± 0.20	± 0.32	± 0.30	± 0.42	± 0.16	± 0.13	± 0.49	± 0.18	± 0.32	
c-22	<0.001	9.6	20.0	18.2	19.8	21.7	25.6	26.3	27.3	27.8	21.1	19.4	-----
			± 0.53	± 0.20	± 0.32	± 0.44	± 0.37	± 0.10	± 0.25	± 0.70	± 0.36	± 0.27	

Appendix 2. cont... Seasonal changes in the fatty acid composition of polar lipids from pike tissues.

			Liver									
			1987					1988				
Fatty Acid	p Value[c]	Seasonal[d] Range wt %	May[b] 5	June 6	July 6	August 7	Sept. 7	Jan. 7	March 7	May 7	June 8	Aug. 6
14:0	<0.001	0.8	0.82[a]	1.35	1.11	1.01	1.08	1.61	1.54	0.81	1.08	1.06
			± 0.14	± 0.06	± 0.06	± 0.03	± 0.07	± 0.13	± 0.07	± 0.14	± 0.05	± 0.06
16:0	0.003	2.6	20.1	19.6	19.7	18.6	18.8	18.1	17.5	19.6	18.7	19.3
			± 0.77	± 0.34	± 0.32	± 0.41	± 0.39	± 0.26	± 0.30	± 0.59	± 0.49	± 0.42
18:0	<0.001	2.8	7.0	8.3	8.5	7.7	7.2	5.8	6.6	6.8	8.6	8.3
			± 0.19	± 0.14	± 0.22	± 0.13	± 0.04	± 0.08	± 0.11	± 0.19	± 0.23	± 0.19
16:1n7	<0.001	3.6	6.7	6.2	6.8	8.0	8.2	9.8	9.6	6.9	6.9	6.9
			± 0.13	± 0.23	± 0.10	± 0.23	± 0.21	± 0.10	± 0.16	± 0.28	± 0.28	± 0.25
18:1n9	<0.001	3.8	12.1	10.6	10.1	10.1	11.7	13.9	12.5	11.8	11.0	10.2
			± 0.40	± 0.41	± 0.25	± 0.15	± 0.21	± 0.30	± 0.25	± 0.27	± 0.49	± 0.28
18:2n6	0.002	0.7	2.1	2.0	2.4	2.7	2.7	2.7	2.3	2.3	2.1	2.7
			± 0.21	± 0.10	± 0.17	± 0.12	± 0.10	± 0.07	± 0.09	± 0.26	± 0.16	± 0.15
20:4n6	<0.001	1.6	8.3	8.7	9.1	8.5	8.8	8.1	8.5	8.3	9.7	9.1
			± 0.23	± 0.07	± 0.23	± 0.20	± 0.07	± 0.09	± 0.10	± 0.17	± 0.16	± 0.24
22:5n6	0.005	0.4	1.5	1.5	1.7	1.5	1.5	1.5	1.5	1.4	1.8	1.8
			± 0.17	± 0.07	± 0.07	± 0.08	± 0.08	± 0.09	± 0.09	± 0.13	± 0.06	± 0.10
18:3n3	<0.001	1.0	1.6	1.5	2.0	2.5	2.3	2.5	2.3	1.9	1.7	1.7
			± 0.08	± 0.08	± 0.18	± 0.16	± 0.12	± 0.06	± 0.13	± 0.17	± 0.12	± 0.09
20:5n3	<0.001	2.8	6.4	8.8	7.5	7.3	6.0	6.5	6.1	6.3	7.4	7.3
			± 0.34	± 0.34	± 0.21	± 0.26	± 0.35	± 0.12	± 0.25	± 0.32	± 0.58	± 0.28
22:5n3	<0.001	0.6	1.2	1.4	1.1	1.1	1.3	1.6	1.4	1.4	1.4	1.7
			± 0.11	± 0.06	± 0.05	± 0.09	± 0.08	± 0.09	± 0.07	± 0.09	± 0.06	± 0.15
22:6n3	<0.001	5.1	29.5	27.0	26.9	27.8	27.1	24.4	26.8	29.5	26.5	26.4
			± 0.46	± 0.46	± 0.28	± 0.38	± 0.48	± 0.46	± 0.47	± 0.46	± 0.31	± 0.63
others	<0.001	1.1	2.5	3.0	3.1	3.3	3.4	3.6	3.4	2.8	3.1	3.4
			± 0.26	± 0.11	± 0.09	± 0.07	± 0.10	± 0.08	± 0.10	± 0.11	± 0.10	± 0.06
SFA	<0.001	3.8	27.9	29.3	29.3	27.3	27.1	25.5	25.7	27.3	28.4	28.6
			± 0.64	± 0.46	± 0.42	± 0.39	± 0.44	± 0.30	± 0.29	± 0.67	± 0.59	± 0.63
MUFA	<0.001	6.9	18.8	16.8	16.9	18.1	19.9	23.7	22.0	18.7	17.9	17.1
			± 0.45	± 0.30	± 0.23	± 0.25	± 0.23	± 0.37	± 0.24	± 0.36	± 0.27	± 0.21
PUFA	<0.001	4.1	50.8	50.9	50.7	51.4	49.6	47.3	48.9	51.2	50.6	50.8
			± 0.51	± 0.48	± 0.54	± 0.24	± 0.48	± 0.59	± 0.44	± 0.49	± 0.70	± 0.55
all n-6	<0.001	1.8	11.9	12.2	13.3	12.7	13.0	12.2	12.3	12.0	13.6	13.7
			± 0.21	± 0.12	± 0.20	± 0.20	± 0.06	± 0.07	± 0.10	± 0.12	± 0.17	± 0.22
all n-3	<0.001	4.1	38.9	38.7	37.5	38.6	36.7	35.1	36.6	39.2	37.0	37.2
			± 0.37	± 0.50	± 0.43	± 0.35	± 0.52	± 0.56	± 0.45	± 0.48	± 0.63	± 0.58
c-16	<0.001	2.3	26.8	25.7	26.5	26.6	27.1	27.9	27.1	26.5	25.6	26.3
			± 0.77	± 0.27	± 0.26	± 0.36	± 0.28	± 0.27	± 0.31	± 0.47	± 0.28	± 0.22
c-18	0.002	2.3	22.8	22.5	23.0	23.0	23.9	24.8	23.8	22.9	23.4	22.9
			± 0.45	± 0.38	± 0.44	± 0.32	± 0.24	± 0.21	± 0.27	± 0.63	± 0.32	± 0.32
c-20	<0.001	2.9	14.8	17.5	16.6	15.8	14.8	14.6	14.6	14.6	17.1	16.4
			± 0.29	± 0.35	± 0.28	± 0.26	± 0.35	± 0.20	± 0.27	± 0.25	± 0.55	± 0.35
c-22	<0.001	4.9	32.3	30.0	29.7	30.3	29.8	27.5	29.7	32.4	29.7	30.0
			± 0.51	± 0.41	± 0.34	± 0.31	± 0.44	± 0.40	± 0.44	± 0.39	± 0.29	± 0.48

Appendix 2. cont... Seasonal changus in the fatty acid composition of polar lipids from pike tissues.

			Muscle									
			1987					1988				
Fatty Acid	p Value[c]	Seasonal[d] Range wt %	May[b] 5	June 7	July 6	August 7	Sept. 6	Jan. 6	March 7	May 7	June 8	Aug. 6
14:0	<0.001	0.42	0.98[a] ± 0.07	0.98 ± 0.05	0.70 ± 0.03	0.61 ± 0.05	0.56 ± 0.04	0.76 ± 0.03	0.79 ± 0.02	0.76 ± 0.05	0.74 ± 0.04	0.60 ± 0.05
16:0	<0.001	3.2	18.1 ± 0.28	19.5 ± 0.24	19.5 ± 0.39	19.6 ± 0.24	18.6 ± 0.33	17.5 ± 0.19	16.6 ± 0.13	17.5 ± 0.24	18.4 ± 0.17	19.8 ± 0.22
18:0	<0.001	1.1	6.5 ± 0.08	7.3 ± 0.11	7.1 ± 0.02	6.6 ± 0.06	6.9 ± 0.13	6.2 ± 0.05	6.2 ± 0.03	6.4 ± 0.10	7.2 ± 0.11	7.2 ± 0.09
16:1n7	0.004	1.3	4.5 ± 0.17	4.1 ± 0.29	3.7 ± 0.07	4.2 ± 0.28	4.2 ± 0.14	4.6 ± 0.13	5.0 ± 0.11	4.4 ± 0.17	4.4 ± 0.27	3.8 ± 0.18
18:1n9	0.029	1.2	10.0 ± 0.41	10.1 ± 0.20	9.4 ± 0.25	9.7 ± 0.32	9.1 ± 0.17	10.0 ± 0.26	9.6 ± 0.33	8.9 ± 0.20	9.7 ± 0.15	9.3 ± 0.29
18:2n6	0.003	0.6	2.6 ± 0.17	2.4 ± 0.07	2.1 ± 0.04	2.5 ± 0.11	2.4 ± 0.08	2.6 ± 0.10	2.6 ± 0.05	2.7 ± 0.11	2.3 ± 0.09	2.7 ± 0.24
20:4n6	0.545	0.9	7.8 ± 0.38	7.5 ± 0.30	7.4 ± 0.31	6.9 ± 0.11	7.4 ± 0.22	7.4 ± 0.30	7.7 ± 0.20	7.7 ± 0.33	7.5 ± 0.21	7.4 ± 0.11
22:5n6	<0.001	0.6	1.8 ± 0.11	1.6 ± 0.04	1.9 ± 0.06	1.8 ± 0.06	1.9 ± 0.07	2.1 ± 0.06	2.2 ± 0.03	2.1 ± 0.05	1.9 ± 0.06	1.9 ± 0.09
18:3n3	<0.001	0.8	2.0 ± 0.15	1.6 ± 0.06	1.5 ± 0.05	2.0 ± 0.13	1.8 ± 0.08	2.2 ± 0.08	2.2 ± 0.05	2.2 ± 0.10	1.5 ± 0.05	1.4 ± 0.07
20:5n3	0.026	0.7	7.4 ± 0.31	6.9 ± 0.23	7.3 ± 0.11	7.6 ± 0.09	7.1 ± 0.09	7.3 ± 0.15	7.5 ± 0.11	7.0 ± 0.22	6.9 ± 0.14	7.0 ± 0.24
22:5n3	0.005	0.5	2.4 ± 0.24	2.0 ± 0.06	2.1 ± 0.08	2.1 ± 0.06	2.2 ± 0.05	2.3 ± 0.07	2.5 ± 0.09	2.3 ± 0.08	2.2 ± 0.07	2.2 ± 0.09
22:6n3	0.305	2.4	31.8 ± 1.06	31.5 ± 0.25	33.1 ± 0.26	32.3 ± 0.80	33.8 ± 0.89	32.8 ± 0.76	33.3 ± 0.87	33.9 ± 0.54	33.3 ± 0.40	32.5 ± 1.18
others	0.003	0.6	4.2 ± 0.19	4.5 ± 0.08	4.3 ± 0.09	4.0 ± 0.04	3.9 ± 0.17	4.1 ± 0.10	3.9 ± 0.12	4.0 ± 0.08	4.1 ± 0.06	4.2 ± 0.09
SFA	<0.001	4.2	25.5 ± 0.33	27.8 ± 0.23	27.3 ± 0.38	26.8 ± 0.29	26.1 ± 0.49	24.5 ± 0.24	23.6 ± 0.13	24.7 ± 0.34	26.3 ± 0.24	27.6 ± 0.23
MUFA	0.053	1.5	14.5 ± 0.56	14.2 ± 0.45	13.1 ± 0.25	13.9 ± 0.54	13.4 ± 0.29	14.6 ± 0.31	14.6 ± 0.40	13.3 ± 0.35	14.1 ± 0.38	13.2 ± 0.45
PUFA	<0.001	4.5	55.8 ± 0.77	53.5 ± 0.45	55.4 ± 0.55	55.3 ± 0.76	56.6 ± 0.89	56.7 ± 0.53	57.9 ± 0.44	58.0 ± 0.66	55.5 ± 0.45	55.0 ± 0.52
all n-6	0.018	1.3	12.3 ± 0.48	11.6 ± 0.30	11.3 ± 0.34	11.2 ± 0.09	11.7 ± 0.21	12.2 ± 0.37	12.5 ± 0.26	12.5 ± 0.40	11.6 ± 0.16	12.0 ± 0.35
all n-3	0.003	3.5	43.5 ± 0.63	42.0 ± 0.26	44.0 ± 0.37	44.1 ± 0.74	44.9 ± 0.88	44.6 ± 0.64	45.5 ± 0.67	45.4 ± 0.46	43.9 ± 0.42	43.0 ± 0.81
c-16	<0.001	2.2	22.6 ± 0.37	23.6 ± 0.26	23.2 ± 0.35	23.8 ± 0.38	22.9 ± 0.45	22.2 ± 0.28	21.6 ± 0.11	21.9 ± 0.35	22.7 ± 0.33	23.6 ± 0.22
c-18	0.302	1.4	21.1 ± 0.33	21.4 ± 0.35	20.0 ± 0.23	20.8 ± 0.54	20.3 ± 0.39	21.0 ± 0.38	20.6 ± 0.41	20.3 ± 0.26	20.7 ± 0.26	20.7 ± 0.56
c-20	0.765	0.9	15.2 ± 0.61	14.4 ± 0.41	14.7 ± 0.36	14.6 ± 0.19	14.5 ± 0.25	14.7 ± 0.38	15.1 ± 0.26	14.7 ± 0.54	14.3 ± 0.23	14.3 ± 0.32
c-22	0.035	3.3	36.0 ± 0.89	35.1 ± 0.29	37.1 ± 0.29	36.2 ± 0.86	38.0 ± 0.91	37.2 ± 0.73	38.0 ± 0.77	38.4 ± 0.49	37.4 ± 0.48	36.5 ± 1.04

Appendix 2. cont... Seasonal changes in the fatty acid composition of polar lipids from pike tissues.

			Adipopancreatic tissue									
		Seasonal[d]	1987					1988				
Fatty Acid	p Value[c]	Range wt %	May[b]	June	July	August	Sept.	Jan.	March	May	June	Aug.
			5	7	6	7	7	7	7	7	8	6
14:0	0.075	0.5	1.4[a]	1.6	1.8	1.5	1.4	1.6	1.4	1.3	1.4	1.5
			± 0.10	± 0.13	± 0.22	± 0.09	± 0.08	± 0.05	± 0.03	± 0.09	± 0.08	± 0.09
16:0	<0.001	2.9	16.2	17.4	17.3	17.1	17.1	14.7	14.5	15.6	16.7	16.0
			± 0.21	± 0.43	± 0.32	± 0.26	± 0.23	± 0.19	± 0.12	± 0.14	± 0.21	± 0.39
18:0	<0.001	2.8	8.1	9.3	9.8	9.1	9.5	7.2	7.6	8.0	10.0	9.6
			± 0.18	± 0.08	± 0.25	± 0.08	± 0.20	± 0.08	± 0.04	± 0.16	± 0.14	± 0.17
16:1n7	<0.001	3.6	8.9	7.6	8.2	8.4	9.0	11.2	11.1	10.0	9.2	9.2
			± 0.26	± 0.37	± 0.57	± 0.21	± 0.34	± 0.16	± 0.10	± 0.41	± 0.43	± 0.46
18:1n9	0.015	1.9	14.2	13.7	13.0	12.5	13.3	14.4	13.8	13.6	14.3	13.4
			± 0.63	± 0.61	± 0.65	± 0.17	± 0.32	± 0.09	± 0.16	± 0.10	± 0.41	± 0.20
18:2n6	<0.001	1.0	3.1	2.9	3.2	3.5	3.5	3.5	3.2	3.4	3.2	3.9
			± 0.19	± 0.06	± 0.15	± 0.16	± 0.07	± 0.09	± 0.08	± 0.14	± 0.16	± 0.18
20:4n6	0.509	1.4	10.2	10.1	9.1	9.7	9.8	9.3	10.5	10.1	10.1	10.1
			± 0.46	± 0.53	± 0.71	± 0.31	± 0.35	± 0.30	± 0.22	± 0.45	± 0.43	± 0.35
22:5n6	0.040	0.6	1.4	1.7	1.9	1.7	1.6	1.6	1.6	1.5	1.7	2.0
			± 0.18	± 0.20	± 0.14	± 0.11	± 0.07	± 0.04	± 0.04	± 0.08	± 0.05	± 0.11
18:3n3	<0.001	1.4	2.9	2.2	2.6	3.1	2.9	3.6	3.3	3.2	2.5	2.6
			± 0.16	± 0.11	± 0.20	± 0.23	± 0.12	± 0.11	± 0.07	± 0.08	± 0.12	± 0.16
20:5n3	<0.001	1.9	7.5	7.2	6.8	7.6	6.9	8.6	8.7	7.9	7.4	7.5
			± 0.52	± 0.35	± 0.36	± 0.17	± 0.22	± 0.20	± 0.14	± 0.28	± 0.18	± 0.19
22:5n3	<0.001	0.6	2.0	2.0	1.6	1.6	1.6	2.0	2.2	2.1	1.9	2.0
			± 0.21	± 0.13	± 0.09	± 0.03	± 0.03	± 0.05	± 0.02	± 0.09	± 0.05	± 0.06
22:6n3	0.003	2.1	19.8	18.6	19.8	19.9	19.5	18.0	18.4	19.7	17.8	18.2
			± 0.60	± 0.56	± 0.67	± 0.44	± 0.60	± 0.35	± 0.23	± 0.44	± 0.45	± 0.41
others	<0.001	2.2	4.3	5.8	4.8	4.1	4.0	4.4	3.7	3.6	3.7	4.1
			± 0.50	± 0.74	± 0.46	± 0.29	± 0.13	± 0.11	± 0.06	± 0.15	± 0.11	± 0.17
SFA	<0.001	5.4	25.7	28.3	28.9	27.8	27.9	23.5	23.5	24.9	28.1	27.1
			± 0.28	± 0.36	± 0.43	± 0.26	± 0.37	± 0.17	± 0.16	± 0.14	± 0.31	± 0.49
MUFA	<0.001	4.7	23.1	21.3	21.2	20.9	22.2	25.6	24.9	23.5	23.5	22.6
			± 0.83	± 0.79	± 1.09	± 0.32	± 0.56	± 0.19	± 0.17	± 0.48	± 0.65	± 0.57
PUFA	0.011	3.4	46.9	44.6	45.1	47.2	45.8	46.6	47.9	48.0	44.6	46.1
			± 1.23	± 1.09	± 1.33	± 0.40	± 0.84	± 0.29	± 0.26	± 0.65	± 0.80	± 0.32
all n-6	0.075	1.8	14.7	14.7	14.2	14.9	15.0	14.4	15.2	15.0	15.0	16.0
			± 0.46	± 0.37	± 0.62	± 0.16	± 0.28	± 0.20	± 0.15	± 0.42	± 0.32	± 0.22
all n-3	<0.001	3.4	32.3	30.0	30.8	32.3	30.8	32.1	32.6	33.0	29.6	30.2
			± 0.84	± 0.82	± 0.86	± 0.32	± 0.81	± 0.15	± 0.21	± 0.34	± 0.53	± 0.20
c-16	0.404	1.0	25.0	25.0	25.5	25.6	26.0	25.9	25.6	25.6	25.9	25.3
			± 0.29	± 0.19	± 0.62	± 0.15	± 0.34	± 0.19	± 0.18	± 0.52	± 0.44	± 0.16
c-18	0.006	2.1	28.3	28.0	28.6	28.3	29.2	28.7	27.9	28.1	30.0	29.5
			± 0.41	± 0.51	± 0.78	± 0.44	± 0.38	± 0.20	± 0.20	± 0.27	± 0.41	± 0.17
c-20	0.047	3.2	17.8	17.2	16.0	17.3	16.7	17.9	19.2	18.0	17.5	17.6
			± 0.91	± 0.83	± 0.95	± 0.42	± 0.47	± 0.37	± 0.26	± 0.55	± 0.54	± 0.37
c-22	0.006	2.0	23.1	22.3	23.2	23.2	22.7	21.6	22.2	23.4	21.4	22.2
			± 0.46	± 0.32	± 0.66	± 0.39	± 0.61	± 0.31	± 0.24	± 0.36	± 0.46	± 0.27

Appendix 3. Seasonal changes in the fatty acid composition of total lipids from pike tissues. Mean ± SE

								Ovary					
			1987					1988					
Fatty Acid	p Value[c]	Seasonal[b] Range wt %	May	June[b] 6	July 6	August 7	Sept. 7	Jan. 7	March 7	May[e] 2	May[f] 4	June 8	Aug.
16:0	<0.001	3.7	-----	19.2[a] ± 0.23	20.2 ± 0.15	19.3 ± 0.21	18.6 ± 0.21	16.6 ± 0.12	16.5 ± 0.15	16.8 ± 0.16	16.8 ± 0.14	18.5 ± 0.23	-----
18:0	<0.001	4.7	-----	9.8 ± 0.05	8.9 ± 0.13	7.2 ± 0.14	6.3 ± 0.12	5.3 ± 0.05	5.5 ± 0.06	5.2 ± 0.06	8.6 ± 0.27	9.9 ± 0.13	-----
16:1n7	<0.001	3.9	-----	8.7 ± 0.29	9.3 ± 0.18	10.0 ± 0.17	10.1 ± 0.19	12.1 ± 0.11	12.6 ± 0.11	12.5 ± 0.17	10.2 ± 0.44	9.9 ± 0.22	-----
18:1n9	<0.001	4.9	-----	15.0 ± 0.27	15.0 ± 0.23	14.5 ± 0.18	15.1 ± 0.56	19.4 ± 0.22	18.7 ± 0.25	18.3 ± 0.13	16.1 ± 0.31	15.1 ± 0.38	-----
18:2n6	<0.001	1.5	-----	2.4 ± 0.07	2.5 ± 0.07	2.9 ± 0.15	3.2 ± 0.11	3.8 ± 0.06	3.7 ± 0.07	3.7 ± 0.21	2.7 ± 0.11	2.3 ± 0.06	-----
20:4n6	<0.001	6.3	-----	12.4 ± 0.29	10.2 ± 0.16	9.0 ± 0.28	8.3 ± 0.21	6.3 ± 0.09	6.1 ± 0.05	6.3 ± 0.28	11.9 ± 0.39	11.6 ± 0.27	-----
22:5n6	<0.001	0.4	-----	1.3 ± 0.04	1.5 ± 0.04	1.4 ± 0.05	1.5 ± 0.07	1.3 ± 0.01	1.3 ± 0.02	1.2 ± 0.12	1.6 ± 0.05	1.6 ± 0.05	-----
18:3n3	<0.001	1.7	-----	1.5 ± 0.09	1.8 ± 0.09	2.2 ± 0.18	2.4 ± 0.15	3.0 ± 0.06	3.0 ± 0.09	3.2 ± 0.24	2.2 ± 0.11	1.5 ± 0.05	-----
20:5n3	<0.001	2.0	-----	7.4 ± 0.21	7.6 ± 0.18	8.0 ± 0.23	7.5 ± 0.24	6.1 ± 0.08	6.1 ± 0.13	6.0 ± 0.37	6.2 ± 0.23	7.4 ± 0.28	-----
22:5n3	<0.001	0.6	-----	1.8 ± 0.06	1.5 ± 0.05	1.5 ± 0.07	1.7 ± 0.10	1.7 ± 0.03	1.7 ± 0.05	1.9 ± 0.13	2.1 ± 0.13	1.8 ± 0.05	-----
22:6n3	<0.001	6.1	-----	15.1 ± 0.27	16.4 ± 0.28	19.7 ± 0.49	21.2 ± 0.37	19.6 ± 0.12	20.1 ± 0.19	20.3 ± 0.77	17.1 ± 0.49	15.7 ± 0.26	-----
others	<0.001	1.0	-----	4.2 ± 0.08	3.9 ± 0.06	3.2 ± 0.07	3.3 ± 0.04	3.9 ± 0.07	3.7 ± 0.09	3.6 ± 0.12	3.7 ± 0.09	3.7 ± 0.07	-----
SFA	<0.001	7.4	-----	30.1 ± 0.27	30.3 ± 0.22	27.4 ± 0.29	25.7 ± 0.24	22.9 ± 0.17	22.9 ± 0.14	23.1 ± 0.24	26.2 ± 0.12	29.3 ± 0.30	-----
MUFA	<0.001	7.7	-----	23.7 ± 0.45	24.4 ± 0.31	24.5 ± 0.21	25.3 ± 0.50	31.4 ± 0.19	31.3 ± 0.23	30.8 ± 0.05	26.3 ± 0.64	25.0 ± 0.47	-----
PUFA	<0.001	4.2	-----	42.0 ± 0.42	41.5 ± 0.43	44.9 ± 0.47	45.7 ± 0.59	41.8 ± 0.22	42.1 ± 0.26	42.6 ± 0.31	43.8 ± 0.61	41.9 ± 0.49	-----
all n-6	<0.001	5.0	-----	16.1 ± 0.30	14.2 ± 0.17	13.3 ± 0.21	13.0 ± 0.19	11.4 ± 0.07	11.2 ± 0.04	11.2 ± 0.19	16.2 ± 0.37	15.4 ± 0.23	-----
all n-3	<0.001	6.9	-----	25.9 ± 0.33	27.3 ± 0.31	31.5 ± 0.56	32.8 ± 0.54	30.4 ± 0.18	30.9 ± 0.26	31.4 ± 0.50	27.6 ± 0.37	26.5 ± 0.42	-----
c-16	<0.001	2.5	-----	27.9 ± 0.28	29.5 ± 0.16	29.3 ± 0.20	28.8 ± 0.15	28.7 ± 0.15	29.1 ± 0.14	29.2 ± 0.02	27.0 ± 0.58	28.4 ± 0.30	-----
c-18	<0.001	4.7	-----	28.6 ± 0.34	28.2 ± 0.45	26.8 ± 0.35	27.1 ± 0.70	31.5 ± 0.17	30.9 ± 0.22	30.4 ± 0.26	29.7 ± 0.26	28.8 ± 0.46	-----
c-20	<0.001	7.6	-----	19.8 ± 0.31	17.9 ± 0.33	17.0 ± 0.39	15.8 ± 0.42	12.4 ± 0.15	12.2 ± 0.14	12.3 ± 0.65	18.1 ± 0.25	19.0 ± 0.31	-----
c-22	<0.001	6.0	-----	18.3 ± 0.26	19.3 ± 0.31	22.7 ± 0.49	24.3 ± 0.42	22.6 ± 0.11	23.1 ± 0.20	23.4 ± 0.52	20.7 ± 0.47	19.1 ± 0.27	-----
FA conc. % wet wt.	<0.001	3.29	-----	0.77	0.85	1.29	2.32	3.98	4.06	2.84	0.98	0.83	-----

Appendix 3. cont... Seasonal changes in the fatty acid composition of total lipids from pike tissues.

				Liver								
				1987				1988				
Fatty Acid	p Value[c]	Seasonal[b] Range wt %	May	June[b] 6	July 6	August 7	Sept. 5	Jan. 7	March 7	May 7	June 8	Aug. 6
16:0	<0.001	5.1	-----	15.2[a]	13.2	12.5	14.0	16.9	16.0	17.6	12.9	12.6
				± 0.73	± 0.50	± 0.38	± 0.54	± 0.30	± 0.36	± 0.35	± 0.73	± 0.67
18:0	0.020	1.5	-----	6.9	6.9	6.9	7.5	6.0	6.8	6.6	6.5	6.7
				± 0.24	± 0.26	± 0.21	± 0.16	± 0.07	± 0.13	± 0.28	± 0.27	± 0.33
16:1n7	0.136	2.0	-----	12.8	11.6	12.5	12.7	11.5	12.2	11.4	13.4	13.2
				± 0.45	± 0.46	± 0.23	± 0.54	± 0.13	± 0.31	± 1.28	± 0.64	± 0.26
18:1n9	<0.001	8.0	-----	24.9	22.0	21.3	22.4	17.1	16.9	18.6	24.4	23.2
				± 2.76	± 1.42	± 0.47	± 0.93	± 0.43	± 1.11	± 2.13	± 1.78	± 0.57
18:2n6	<0.001	3.8	-----	4.8	6.3	7.2	6.2	3.4	3.4	3.7	5.3	7.2
				± 0.29	± 0.36	± 0.25	± 0.35	± 0.14	± 0.14	± 0.17	± 0.34	± 0.33
20:4n6	<0.001	1.8	-----	5.5	5.8	5.7	6.4	7.2	7.3	6.6	6.1	6.1
				± 0.39	± 0.28	± 0.21	± 0.22	± 0.08	± 0.23	± 0.41	± 0.20	± 0.31
22:5n6	0.004	0.4	-----	0.9	1.3	1.2	1.1	1.3	1.3	1.1	1.3	1.3
				± 0.11	± 0.09	± 0.04	± 0.46	± 0.09	± 0.07	± 0.05	± 0.06	± 0.04
18:3n3	<0.001	2.5	-----	3.0	4.2	5.2	3.9	2.9	3.0	2.7	3.2	3.4
				± 0.30	± 0.38	± 0.45	± 0.31	± 0.11	± 0.18	± 0.15	± 0.28	± 0.16
20:5n3	0.022	2.1	-----	7.2	6.9	5.9	5.1	6.0	5.5	5.5	6.6	6.8
				± 0.82	± 0.35	± 0.29	± 0.36	± 0.08	± 0.31	± 0.44	± 0.52	± 0.52
22:5n3	<0.001	1.3	-----	2.0	2.2	1.7	1.2	1.5	1.3	1.2	2.1	2.5
				± 0.13	± 0.05	± 0.12	± 0.12	± 0.07	± 0.08	± 0.11	± 0.14	± 0.13
22:6n3	<0.001	9.2	-----	12.6	15.6	15.1	15.5	21.2	21.8	21.4	13.9	13.0
				± 0.92	± 1.26	± 1.22	± 1.10	± 1.34	± 1.31	± 1.14	± 1.28	± 1.30
others	<0.001	1.5	-----	3.9	3.9	4.6	3.5	3.7	3.5	3.1	3.9	3.8
				± 0.21	± 0.17	± 0.27	± 0.14	± 0.08	± 0.10	± 0.11	± 0.09	± 0.16
SFA	<0.001	5.2	-----	22.3	20.3	19.7	22.0	24.2	24.0	24.7	19.7	19.5
				± 0.84	± 0.69	± 0.57	± 0.64	± 0.36	± 0.33	± 0.50	± 0.97	± 1.00
MUFA	0.002	9.3	-----	37.8	33.6	33.8	35.0	28.6	29.0	29.9	37.9	36.4
				± 3.10	± 1.66	± 0.48	± 1.46	± 0.51	± 1.38	± 3.35	± 2.04	± 0.45
PUFA	0.182	7.6	-----	36.0	42.2	42.0	39.5	43.6	43.5	42.3	38.6	40.2
				± 3.56	± 1.94	± 0.56	± 1.21	± 0.48	± 1.28	± 3.29	± 2.09	± 1.35
all n-6	<0.001	3.2	-----	11.3	13.3	14.1	13.7	12.0	12.0	11.4	12.8	14.5
				± 0.75	± 0.46	± 0.19	± 0.16	± 0.08	± 0.20	± 0.59	± 0.49	± 0.18
all n-3	0.017	6.8	-----	24.8	28.9	27.9	25.8	31.6	31.5	30.8	25.8	25.7
				± 2.84	± 1.51	± 0.58	± 1.25	± 0.42	± 1.11	± 2.76	± 1.63	± 1.24
c-16	<0.001	4.2	-----	28.0	24.8	25.0	26.7	28.3	28.1	29.0	26.3	25.8
				± 1.12	± 0.68	± 0.44	± 0.40	± 0.25	± 0.24	± 1.41	± 0.51	± 0.69
c-18	<0.001	11.1	-----	39.7	39.4	40.6	39.9	29.5	30.1	31.6	39.5	40.5
				± 2.33	± 1.21	± 0.82	± 1.48	± 0.53	± 1.23	± 1.77	± 1.28	± 0.84
c-20	0.650	1.6	-----	12.7	12.6	11.6	11.5	13.1	12.7	12.1	12.8	12.9
				± 1.19	± 0.53	± 0.39	± 0.31	± 0.15	± 0.51	± 0.78	± 0.67	± 0.79
c-22	<0.001	8.9	-----	15.5	19.1	18.0	17.9	24.1	24.4	23.8	17.3	16.8
				± 1.84	± 1.18	± 0.86	± 1.54	± 0.36	± 0.86	± 2.39	± 1.02	± 0.88
FA conc. % wet wt.	<0.001	5.84	-----	7.98	6.24	5.48	4.15	2.14	2.15	2.78	6.09	6.05

Appenidx 3. cont... Seasonal changes in the fatty acid composition of total lipids from pike tissues.

			Muscle									
		Seasonal[d]	1987					1988				
Fatty Acid	p Value[c]	Range wt %	May[b] 5	June 6	July 6	August 7	Sept. 6	Jan. 6	March 7	May 7	June 7	Aug. 6
16:0	<0.001	2.4	15.0[a]	17.1	16.9	15.8	15.3	15.4	14.7	15.5	15.7	16.1
			± 0.35	± 0.63	± 0.43	± 0.24	± 0.41	± 0.19	± 0.13	± 0.15	± 0.29	± 0.25
18:0	<0.001	0.7	6.3	6.8	6.7	6.1	6.5	6.2	6.2	6.2	6.8	6.6
			± 0.16	± 0.14	± 0.04	± 0.07	± 0.09	± 0.05	± 0.03	± 0.08	± 0.09	± 0.09
16:1n7	0.020	2.6	11.8	9.6	9.5	11.2	10.9	11.2	12.1	11.0	11.7	11.9
			± 0.27	± 0.90	± 0.67	± 0.29	± 0.87	± 0.45	± 0.32	± 0.60	± 0.62	± 0.16
18:1n9	0.161	2.4	16.1	14.8	13.9	15.0	14.3	14.8	15.2	13.7	15.4	14.6
			± 0.70	± 0.87	± 0.60	± 0.37	± 0.48	± 0.35	± 0.57	± 0.50	± 0.61	± 0.37
18:2n6	0.066	0.9	4.9	4.4	4.1	4.9	4.8	4.5	4.4	4.2	4.2	5.0
			± 0.32	± 0.32	± 0.19	± 0.20	± 0.35	± 0.09	± 0.18	± 0.10	± 0.22	± 0.21
20:4n6	0.036	0.9	5.6	6.1	5.8	5.3	5.5	5.7	5.8	6.2	5.8	5.7
			± 0.16	± 0.22	± 0.19	± 0.12	± 0.22	± 0.16	± 0.07	± 0.26	± 0.18	± 0.12
22:5n6	0.013	0.2	1.4	1.4	1.6	1.4	1.6	1.6	1.6	1.6	1.5	1.5
			± 0.06	± 0.08	± 0.06	± 0.03	± 0.07	± 0.03	± 0.05	± 0.04	± 0.06	± 0.04
18:3n3	0.006	1.1	4.7	3.9	3.8	4.9	4.6	4.6	4.7	4.2	3.8	3.9
			± 0.19	± 0.36	± 0.26	± 0.28	± 0.38	± 0.13	± 0.23	± 0.13	± 0.27	± 0.15
20:5n3	0.099	0.7	6.5	6.7	7.0	6.8	6.3	6.6	7.0	6.8	6.6	6.6
			± 0.36	± 0.17	± 0.12	± 0.17	± 0.15	± 0.12	± 0.13	± 0.10	± 0.17	± 0.11
22:5n3	0.143	0.2	1.9	1.9	2.0	2.0	2.1	2.0	2.0	2.0	2.0	2.1
			± 0.09	± 0.03	± 0.04	± 0.03	± 0.02	± 0.05	± 0.06	± 0.07	± 0.06	± 0.03
22:6n3	0.379	3.9	18.6	19.7	22.0	19.7	21.6	20.7	20.3	22.5	20.5	20.0
			± 0.79	± 1.73	± 1.29	± 0.69	± 1.63	± 0.68	± 1.02	± 0.88	± 1.01	± 0.78
others	<0.001	1.5	6.9	7.2	6.4	6.6	6.3	6.4	5.8	5.7	5.8	5.8
			± 0.23	± 0.48	± 0.19	± 0.18	± 0.36	± 0.11	± 0.10	± 0.20	± 0.25	± 0.17
SFA	<0.001	3.0	21.7	24.3	23.9	22.1	22.1	22.0	21.3	22.1	22.7	22.9
			± 0.51	± 0.81	± 0.48	± 0.34	± 0.50	± 0.23	± 0.17	± 0.22	± 0.35	± 0.33
MUFA	0.085	4.5	27.9	24.3	23.4	26.2	25.2	26.0	27.2	24.7	27.1	26.5
			± 0.91	± 1.67	± 1.11	± 0.62	± 1.34	± 0.59	± 0.85	± 1.07	± 1.07	± 0.48
PUFA	0.148	4.0	43.5	44.1	46.3	45.0	46.4	45.7	45.7	47.5	44.4	44.7
			± 0.83	± 1.37	± 1.01	± 0.74	± 1.21	± 0.70	± 0.86	± 1.14	± 0.78	± 0.46
all n-6	0.286	0.7	11.9	11.9	11.5	11.6	11.9	11.8	11.8	12.0	11.5	12.2
			± 0.38	± 0.19	± 0.14	± 0.09	± 0.14	± 0.17	± 0.13	± 0.37	± 0.12	± 0.18
all n-3	0.144	3.7	31.7	32.3	34.8	33.5	34.5	33.9	33.9	35.4	32.9	32.6
			± 0.91	± 1.36	± 1.00	± 0.74	± 1.31	± 0.67	± 0.92	± 0.83	± 0.76	± 0.59
c-16	0.211	1.7	26.8	26.6	26.4	27.0	26.3	26.6	26.8	26.5	27.3	28.0
			± 0.29	± 0.68	± 0.53	± 0.31	± 0.47	± 0.47	± 0.28	± 0.57	± 0.36	± 0.21
c-18	0.175	3.7	32.0	29.9	28.6	30.9	30.2	30.1	30.5	28.3	30.1	30.0
			± 0.95	± 1.32	± 0.90	± 0.60	± 1.13	± 0.44	± 0.88	± 0.53	± 0.79	± 0.61
c-20	0.035	1.2	12.1	12.8	12.8	12.1	11.8	12.3	12.7	13.0	12.4	12.3
			± 0.49	± 0.24	± 0.17	± 0.22	± 0.32	± 0.22	± 0.16	± 0.34	± 0.21	± 0.21
c-22	0.316	4.2	21.9	23.0	25.5	23.2	25.2	24.3	23.9	26.1	24.0	23.6
			± 0.74	± 1.79	± 1.36	± 0.70	± 1.68	± 0.70	± 1.07	± 0.92	± 1.10	± 0.76
FA conc. % wet wt.	0.081	0.43	0.93	0.76	0.71	0.97	1.12	0.83	0.84	0.69	0.78	0.73

Appendix 3. cont... Seasonal changes in the fatty acid composition of total lipids from pike tissues.

			Adipopancreatic Tissue									
		Seasonal[d]	1987					1988				
Fatty Acid	p Value[c]	Range wt %	May	June[b] 7	July 6	August 7	Sept. 7	Jan. 7	March 7	May 7	June 8	Aug. 6
16:0	<0.001	3.1	-----	15.1[a]	13.5	13.0	13.0	12.6	12.0	12.3	13.0	13.1
				± 0.76	± 0.33	± 0.21	± 0.31	± 0.27	± 0.35	± 0.13	± 0.17	± 0.35
18:0	<0.001	0.6	-----	6.1	5.9	5.6	6.1	5.8	5.6	5.5	5.8	5.8
				± 0.18	± 0.07	± 0.07	± 0.14	± 0.08	± 0.09	± 0.05	± 0.10	± 0.11
16:1n7	<0.001	5.1	-----	15.0	15.3	16.1	15.9	18.8	20.1	20.1	18.4	18.8
				± 0.37	± 0.22	± 0.18	± 0.27	± 0.28	± 0.40	± 0.28	± 0.31	± 0.26
18:1n9	0.162	2.5	-----	19.5	18.3	17.8	18.2	19.3	18.5	18.9	20.3	18.8
				± 1.00	± 1.16	± 0.35	± 0.38	± 0.31	± 0.49	± 0.39	± 0.76	± 0.41
18:2n6	0.047	0.8	-----	6.1	6.2	6.8	6.7	6.6	6.4	6.8	6.1	6.9
				± 0.16	± 0.24	± 0.21	± 0.15	± 0.17	± 0.20	± 0.25	± 0.28	± 0.27
20:4n6	0.104	0.5	-----	4.5	4.3	4.0	4.2	4.0	4.1	4.4	4.3	4.2
				± 0.14	± 0.16	± 0.14	± 0.16	± 0.12	± 0.10	± 0.14	± 0.08	± 0.15
22:5n6	0.050	0.3	-----	1.0	1.4	1.2	1.3	1.1	1.1	1.1	1.1	1.3
				± 1.04	± 1.37	± 1.19	± 1.27	± 1.09	± 1.07	± 1.15	± 1.14	± 1.26
18:3n3	<0.001	1.8	-----	6.0	6.3	7.7	6.8	7.5	7.5	7.1	6.1	5.9
				± 0.24	± 0.27	± 0.47	± 0.28	± 0.33	± 0.22	± 0.16	± 0.24	± 0.12
20:5n3	0.043	1.2	-----	6.8	6.1	6.0	5.6	5.9	6.2	5.9	6.2	5.8
				± 0.26	± 0.28	± 0.32	± 0.13	± 0.10	± 0.15	± 0.36	± 0.22	± 0.21
22:5n3	<0.001	0.8	-----	1.9	2.1	1.9	2.2	1.6	1.6	1.4	2.0	2.0
				± 0.11	± 0.06	± 0.10	± 0.11	± 0.10	± 0.07	± 0.06	± 0.09	± 0.05
22:6n3	<0.001	5.0	-----	10.4	13.0	12.0	12.4	9.0	8.6	8.0	9.8	10.3
				± 0.96	± 0.71	± 0.50	± 0.51	± 0.49	± 0.45	± 0.47	± 0.39	± 0.54
others	0.006	1.4	-----	7.5	7.7	8.0	7.7	7.7	8.3	8.5	7.1	7.1
				± 0.42	± 0.28	± 0.20	± 0.25	± 0.15	± 0.27	± 0.24	± 0.30	± 0.24
SFA	<0.001	3.7	-----	21.3	19.4	18.5	19.1	18.4	17.6	17.8	18.8	18.9
				± 0.92	± 0.37	± 0.23	± 0.42	± 0.34	± 0.42	± 0.15	± 0.17	± 0.45
MUFA	<0.001	5.4	-----	34.5	33.6	33.9	34.1	38.1	38.6	39.0	38.7	37.6
				± 0.80	± 1.12	± 0.44	± 0.33	± 0.27	± 0.29	± 0.28	± 0.66	± 0.38
PUFA	<0.001	2.9	-----	36.7	39.3	39.6	39.2	35.8	35.6	34.7	35.5	36.4
				± 1.20	± 1.06	± 0.33	± 0.44	± 0.30	± 0.44	± 0.23	± 0.36	± 0.50
all n-6	0.044	0.9	-----	11.6	11.9	11.9	12.2	11.8	11.7	12.3	11.5	12.4
				± 0.22	± 0.31	± 0.09	± 0.14	± 0.07	± 0.22	± 0.37	± 0.25	± 0.14
all n-3	<0.001	5.3	-----	25.0	27.4	27.7	26.9	24.0	23.9	22.4	24.0	24.0
				± 1.13	± 0.79	± 0.28	± 0.39	± 0.32	± 0.40	± 0.44	± 0.27	± 0.62
c-16	<0.001	3.6	-----	30.1	28.8	29.0	28.9	31.4	32.1	32.4	31.4	31.9
				± 0.81	± 0.26	± 0.28	± 0.32	± 0.23	± 0.24	± 0.23	± 0.22	± 0.34
c-18	0.546	2.6	-----	37.7	36.7	37.9	37.8	39.3	38.0	38.3	38.2	37.4
				± 0.99	± 0.80	± 0.76	± 0.64	± 0.74	± 0.81	± 0.60	± 0.43	± 0.65
c-20	0.025	1.5	-----	11.4	10.4	10.0	9.9	9.9	10.3	10.3	10.5	10.0
				± 0.21	± 0.39	± 0.42	± 0.25	± 0.20	± 0.23	± 0.34	± 0.27	± 0.33
c-22	<0.001	5.9	-----	13.3	16.4	15.1	15.8	11.7	11.3	10.5	12.9	13.6
				± 1.07	± 0.78	± 0.62	± 0.64	± 0.63	± 0.57	± 0.54	± 0.49	± 0.65
FA conc. wet wt.	0.250	16.8	40.2	56.9	57.4	57.4	53.4	57.5	49.2	45.3	62.1	61.4

Appendix 4. Seasonal changes in the fatty acid composition of somatic tissue neutral lipids of pike. Mean ± SE

Fatty Acid	p Value[c]	Seasonal[d] Range wt %	1987					1988				
			May	June[b] 6	July 6	August 7	Sept. 4	Jan. 6	March 7	May 7	June 7	Aug. 6
16:0	<0.001	3.1	-----	15.4[a] ± 0.76	13.7 ± 0.23	13.0 ± 0.15	12.8 ± 0.03	12.9 ± 0.27	12.3 ± 0.23	12.5 ± 0.17	12.9 ± 0.20	13.0 ± 0.29
18:0	<0.001	0.6	-----	6.3 ± 0.13	6.1 ± 0.05	5.7 ± 0.06	6.2 ± 0.05	5.9 ± 0.05	5.9 ± 0.07	5.7 ± 0.03	5.9 ± 0.11	5.9 ± 0.10
16:1n7	<0.001	5.2	-----	14.8 ± 0.18	14.8 ± 0.15	15.7 ± 0.14	15.8 ± 0.25	18.3 ± 0.28	19.6 ± 0.37	20.0 ± 0.19	18.0 ± 0.28	18.2 ± 0.21
18:1n9	0.018	2.8	-----	21.2 ± 1.15	19.0 ± 0.75	18.4 ± 0.26	18.7 ± 0.35	19.7 ± 0.34	19.5 ± 0.38	19.4 ± 0.28	21.1 ± 0.83	19.4 ± 0.22
18:2n6	0.002	1.1	-----	5.9 ± 0.20	6.2 ± 0.20	6.7 ± 0.16	6.7 ± 0.15	6.5 ± 0.18	6.3 ± 0.15	6.5 ± 0.25	5.9 ± 0.19	7.0 ± 0.16
20:4n6	0.017	0.5	-----	4.5 ± 0.10	4.4 ± 0.09	4.1 ± 0.10	4.2 ± 0.18	4.0 ± 0.08	4.0 ± 0.06	4.2 ± 0.10	4.3 ± 0.07	4.3 ± 0.13
22:5n6	0.002	0.3	-----	1.0 ± 0.09	1.3 ± 0.07	1.2 ± 0.04	1.3 ± 0.03	1.1 ± 0.05	1.1 ± 0.04	1.1 ± 0.03	1.1 ± 0.06	1.2 ± 0.03
18:3n3	<0.001	1.8	-----	5.5 ± 0.26	6.0 ± 0.19	7.3 ± 0.35	6.5 ± 0.14	7.3 ± 0.33	7.3 ± 0.17	6.9 ± 0.12	5.8 ± 0.17	5.7 ± 0.08
20:5n3	0.131	0.9	-----	6.5 ± 0.23	6.3 ± 0.18	6.2 ± 0.22	5.6 ± 0.26	5.8 ± 0.11	6.2 ± 0.16	6.1 ± 0.19	6.3 ± 0.19	6.1 ± 0.14
22:5n3	<0.001	0.7	-----	1.8 ± 0.04	2.1 ± 0.04	1.9 ± 0.05	2.1 ± 0.04	1.6 ± 0.07	1.6 ± 0.04	1.4 ± 0.03	2.0 ± 0.04	2.1 ± 0.03
22:6n3	<0.001	4.3	-----	9.6 ± 0.83	12.5 ± 0.42	12.0 ± 0.31	12.4 ± 0.31	9.0 ± 0.37	8.2 ± 0.22	7.9 ± 0.28	9.8 ± 0.34	10.3 ± 0.32
others	<0.001	1.4	-----	7.5 ± 0.41	7.5 ± 0.22	7.9 ± 0.15	7.7 ± 0.24	7.9 ± 0.18	8.0 ± 0.23	8.2 ± 0.07	6.8 ± 0.32	6.8 ± 0.18
SFA	<0.001	3.5	-----	21.7 ± 0.88	19.8 ± 0.25	18.7 ± 0.18	19.0 ± 0.08	18.8 ± 0.31	18.2 ± 0.28	18.2 ± 0.16	18.9 ± 0.22	18.9 ± 0.38
MUFA	<0.001	5.6	-----	36.0 ± 1.03	33.8 ± 0.70	34.1 ± 0.28	34.5 ± 0.34	37.9 ± 0.07	39.1 ± 0.23	39.4 ± 0.17	39.1 ± 0.79	37.6 ± 0.21
PUFA	<0.001	5.2	-----	34.8 ± 1.43	38.8 ± 0.64	39.3 ± 0.29	38.8 ± 0.32	35.4 ± 0.21	34.7 ± 0.28	34.1 ± 0.32	35.2 ± 0.50	36.7 ± 0.40
all n-6	0.002	1.2	-----	11.4 ± 0.35	11.9 ± 0.22	12.0 ± 0.07	12.2 ± 0.16	11.6 ± 0.08	11.4 ± 0.16	11.9 ± 0.35	11.3 ± 0.18	12.5 ± 0.04
all n-3	<0.001	5.0	-----	23.4 ± 1.14	27.0 ± 0.46	27.3 ± 0.26	26.6 ± 0.21	23.8 ± 0.22	23.4 ± 0.19	22.3 ± 0.30	23.9 ± 0.34	24.1 ± 0.43
c-16	<0.001	4.0	-----	30.3 ± 0.62	28.5 ± 0.31	28.7 ± 0.16	28.6 ± 0.21	31.1 ± 0.15	32.0 ± 0.22	32.5 ± 0.23	31.0 ± 0.13	31.2 ± 0.35
c-18	0.269	2.1	-----	38.9 ± 0.93	37.3 ± 0.50	38.1 ± 0.50	38.1 ± 0.15	39.4 ± 0.66	38.9 ± 0.53	38.5 ± 0.41	38.7 ± 0.51	37.9 ± 0.36
c-20	0.064	1.2	-----	11.0 ± 0.30	10.7 ± 0.24	10.3 ± 0.29	9.8 ± 0.42	9.8 ± 0.16	10.3 ± 0.21	10.3 ± 0.19	10.6 ± 0.24	10.4 ± 0.25
c-22	<0.001	5.5	-----	12.4 ± 0.93	15.9 ± 0.48	15.1 ± 0.38	15.8 ± 0.32	11.7 ± 0.48	10.9 ± 0.28	10.4 ± 0.32	12.9 ± 0.41	13.7 ± 0.37
FA conc. % wet wt.	0.241	0.7	-----	1.7	1.2	1.5	1.3	1.2	1.1	1.0	1.6	1.3

Appendix 5. Seasonal changes in the fatty acid composition of somatic tissue polar lipids of pike. Mean ± SE

Fatty Acid	p Value[c]	Seasonal[d] Range wt %	1987					1988				
			May	June[b] 6	July 6	August 7	Sept. 6	Jan. 6	March 7	May 7	June 8	Aug. 6
16:0	<0.001	3.0	-----	19.4[a]	19.5	19.5	18.6	17.6	16.7	17.7	18.4	19.7
				± 0.25	± 0.36	± 0.22	± 0.30	± 0.19	± 0.13	± 0.22	± 0.17	± 0.22
18:0	<0.001	1.2	-----	7.4	7.2	6.7	7.0	6.2	6.3	6.5	7.4	7.3
				± 0.12	± 0.03	± 0.05	± 0.12	± 0.03	± 0.03	± 0.09	± 0.11	± 0.10
16:1n7	<0.001	1.9	-----	4.3	4.0	4.6	4.8	5.8	5.9	4.8	4.6	4.2
				± 0.31	± 0.06	± 0.27	± 0.16	± 0.10	± 0.08	± 0.16	± 0.25	± 0.18
18:1n9	<0.001	1.5	-----	10.1	9.5	9.8	9.5	10.8	10.2	9.3	9.9	9.5
				± 0.15	± 0.24	± 0.29	± 0.17	± 0.26	± 0.29	± 0.20	± 0.14	± 0.26
18:2n6	0.003	0.7	-----	2.4	2.1	2.5	2.5	2.7	2.6	2.7	2.3	2.8
				± 0.07	± 0.05	± 0.11	± 0.08	± 0.08	± 0.03	± 0.13	± 0.09	± 0.22
20:4n6	0.427	0.8	-----	7.8	7.5	7.1	7.6	7.6	7.9	7.8	7.7	7.6
				± 0.30	± 0.31	± 0.11	± 0.20	± 0.26	± 0.18	± 0.28	± 0.20	± 0.10
22:5n6	<0.001	0.5	-----	1.6	1.9	1.8	1.9	2.0	2.1	2.0	1.9	1.9
				± 0.04	± 0.06	± 0.05	± 0.06	± 0.03	± 0.04	± 0.05	± 0.05	± 0.09
18:3n3	<0.001	0.9	-----	1.6	1.5	2.1	1.9	2.3	2.2	2.2	1.5	1.4
				± 0.05	± 0.05	± 0.14	± 0.09	± 0.08	± 0.05	± 0.10	± 0.05	± 0.07
20:5n3	0.027	0.7	-----	7.0	7.3	7.6	7.0	7.2	7.2	6.9	6.9	7.0
				± 0.22	± 0.11	± 0.08	± 0.09	± 0.12	± 0.07	± 0.21	± 0.13	± 0.23
22:5n3	0.006	0.3	-----	2.0	2.1	2.0	2.1	2.2	2.3	2.2	2.1	2.1
				± 0.07	± 0.07	± 0.05	± 0.05	± 0.07	± 0.06	± 0.08	± 0.07	± 0.08
22:6n3	0.246	2.2	-----	31.2	32.5	31.7	32.8	30.9	31.9	33.1	32.5	31.8
				± 0.11	± 0.26	± 0.72	± 0.87	± 0.69	± 0.68	± 0.50	± 0.36	± 1.10
others	<0.001	0.6	-----	4.4	4.2	3.9	3.8	4.0	3.8	3.9	4.0	4.1
				± 0.08	± 0.08	± 0.03	± 0.15	± 0.09	± 0.10	± 0.07	± 0.06	± 0.08
SFA	<0.001	3.8	-----	27.8	27.4	26.9	26.3	24.7	24.0	25.0	26.5	27.7
				± 0.25	± 0.36	± 0.27	± 0.45	± 0.24	± 0.12	± 0.33	± 0.24	± 0.24
MUFA	<0.001	3.1	-----	14.4	13.5	14.3	14.3	16.6	16.1	14.1	14.6	13.6
				± 0.43	± 0.24	± 0.50	± 0.30	± 0.33	± 0.32	± 0.34	± 0.33	± 0.40
PUFA	0.003	3.7	-----	53.4	54.8	54.8	55.6	54.7	56.2	57.1	54.9	54.5
				± 0.38	± 0.54	± 0.69	± 0.84	± 0.53	± 0.39	± 0.64	± 0.39	± 0.49
all n-6	0.020	1.2	-----	11.8	11.5	11.4	11.9	12.2	12.5	12.6	11.8	12.2
				± 0.30	± 0.33	± 0.08	± 0.18	± 0.29	± 0.22	± 0.35	± 0.15	± 0.33
all n-3	0.042	2.9	-----	41.6	43.3	43.4	43.7	42.5	43.7	44.5	43.1	42.3
				± 0.23	± 0.38	± 0.68	± 0.86	± 0.61	± 0.58	± 0.44	± 0.38	± 0.75
c-16	0.004	1.5	-----	23.7	23.5	24.0	23.4	23.3	22.6	22.5	23.0	23.9
				± 0.23	± 0.33	± 0.36	± 0.42	± 0.27	± 0.12	± 0.33	± 0.29	± 0.21
c-18	0.175	1.5	-----	21.5	20.4	21.1	20.8	21.9	21.3	20.7	21.1	21.0
				± 0.30	± 0.23	± 0.49	± 0.39	± 0.35	± 0.33	± 0.26	± 0.24	± 0.51
c-20	0.954	0.6	-----	14.7	14.8	14.7	14.5	14.7	15.1	14.8	14.6	14.6
				± 0.43	± 0.35	± 0.18	± 0.20	± 0.33	± 0.18	± 0.48	± 0.17	± 0.30
c-22	0.093	2.7	-----	34.7	36.4	35.5	36.8	35.1	36.3	37.4	36.5	35.8
				± 0.12	± 0.30	± 0.77	± 0.89	± 0.67	± 0.60	± 0.44	± 0.43	± 0.96
FA conc. % wet wt.	<0.001	0.14	-----	0.34	0.33	0.36	0.43	0.47	0.46	0.41	0.36	0.33

Appendix 6. Seasonal changes in the fatty acid composition of combined neutral lipids in ovarian and somatic tissues of pike. Mean ± SE

Fatty Acid	p Value[c]	Seasonal[d] Range wt %	1987					1988					
			May	June[b] 6	July 6	August 7	Sept. 4	Jan. 6	March 7	May[e] 2	May[f] 4	June 7	Aug.
16:0	<0.001	3.6	-----	15.4[a] ± 0.76	13.7 ± 0.23	13.0 ± 0.15	12.8 ± 0.07	12.4 ± 0.21	11.8 ± 0.20	11.8 ± 0.33	12.7 ± 0.25	12.9 ± 0.20	-----
18:0	<0.001	0.6	-----	6.3 ± 0.13	6.1 ± 0.05	5.7 ± 0.06	6.2 ± 0.05	6.1 ± 0.07	6.1 ± 0.10	6.0 ± 0.12	5.7 ± 0.04	5.9 ± 0.11	-----
16:1n7	<0.001	5.0	-----	14.8 ± 0.18	14.8 ± 0.15	15.7 ± 0.14	15.8 ± 0.26	18.1 ± 0.25	19.4 ± 0.29	19.4 ± 0.42	19.8 ± 0.28	18.0 ± 0.28	-----
18:1n9	<0.001	4.6	-----	21.2 ± 1.15	19.0 ± 0.75	18.4 ± 0.26	18.7 ± 0.36	21.5 ± 0.55	22.3 ± 0.44	23.0 ± 0.83	19.7 ± 0.46	21.1 ± 0.83	-----
18:2n6	0.033	0.8	-----	5.9 ± 0.20	6.2 ± 0.20	6.7 ± 0.16	6.7 ± 0.16	6.5 ± 0.16	6.3 ± 0.13	6.4 ± 0.36	6.5 ± 0.44	5.9 ± 0.19	-----
20:4n6	<0.001	0.7	-----	4.5 ± 0.10	4.4 ± 0.09	4.1 ± 0.10	4.2 ± 0.18	3.8 ± 0.06	3.8 ± 0.03	4.1 ± 0.04	4.2 ± 0.18	4.3 ± 0.07	-----
22:5n6	<0.001	0.3	-----	1.0 ± 0.09	1.3 ± 0.07	1.2 ± 0.04	1.3 ± 0.03	1.0 ± 0.04	1.0 ± 0.03	1.0 ± 0.00	1.1 ± 0.06	1.1 ± 0.06	-----
18:3n3	<0.001	1.7	-----	5.5 ± 0.26	6.0 ± 0.19	7.2 ± 0.35	6.4 ± 0.14	6.9 ± 0.33	6.6 ± 0.19	6.3 ± 0.03	6.6 ± 0.08	5.8 ± 0.17	-----
20:5n3	<0.001	1.1	-----	6.5 ± 0.23	6.3 ± 0.18	6.2 ± 0.22	5.6 ± 0.25	5.4 ± 0.11	5.5 ± 0.08	5.4 ± 0.42	6.0 ± 0.30	6.3 ± 0.19	-----
22:5n3	<0.001	0.8	-----	1.8 ± 0.04	2.1 ± 0.04	1.9 ± 0.05	2.1 ± 0.04	1.5 ± 0.06	1.5 ± 0.04	1.3 ± 0.08	1.4 ± 0.02	2.0 ± 0.04	-----
22:6n3	<0.001	4.4	-----	9.6 ± 0.83	12.6 ± 0.42	12.0 ± 0.31	12.6 ± 0.31	9.4 ± 0.33	8.9 ± 0.23	8.6 ± 0.47	8.2 ± 0.45	9.9 ± 0.34	-----
others	0.015	1.4	-----	7.5 ± 0.41	7.5 ± 0.22	7.8 ± 0.15	7.6 ± 0.25	7.2 ± 0.20	6.9 ± 0.22	6.7 ± 0.55	8.1 ± 0.08	6.8 ± 0.32	-----
SFA	<0.001	3.9	-----	21.7 ± 0.88	19.8 ± 0.25	18.7 ± 0.18	19.0 ± 0.12	18.5 ± 0.25	17.9 ± 0.25	17.8 ± 0.21	18.4 ± 0.21	18.9 ± 0.22	-----
MUFA	<0.001	8.5	-----	36.0 ± 1.03	33.8 ± 0.70	34.1 ± 0.28	34.5 ± 0.36	39.7 ± 0.33	41.6 ± 0.30	42.3 ± 0.42	39.5 ± 0.29	39.1 ± 0.79	-----
PUFA	<0.001	6.2	-----	34.8 ± 1.43	38.8 ± 0.64	39.4 ± 0.29	38.9 ± 0.29	34.6 ± 0.33	33.6 ± 0.30	33.2 ± 0.34	34.0 ± 0.55	35.2 ± 0.50	-----
all n-6	0.014	1.2	-----	11.4 ± 0.35	11.9 ± 0.22	12.0 ± 0.07	12.2 ± 0.15	11.4 ± 0.10	11.0 ± 0.15	11.5 ± 0.40	11.8 ± 0.61	11.3 ± 0.18	-----
all n-3	<0.001	5.6	-----	23.4 ± 1.14	27.0 ± 0.46	27.3 ± 0.26	26.7 ± 0.19	23.2 ± 0.28	22.6 ± 0.19	21.7 ± 0.06	22.2 ± 0.51	23.9 ± 0.34	-----
c-16	<0.001	4.0	-----	30.3 ± 0.62	28.5 ± 0.31	28.7 ± 0.16	28.6 ± 0.18	30.6 ± 0.14	31.1 ± 0.18	31.1 ± 0.75	32.5 ± 0.39	31.0 ± 0.13	-----
c-18	<0.001	4.5	-----	38.9 ± 0.93	37.3 ± 0.50	38.0 ± 0.50	38.0 ± 0.17	41.0 ± 0.64	41.3 ± 0.48	41.8 ± 1.29	38.5 ± 0.73	38.7 ± 0.52	-----
c-20	<0.001	1.7	-----	11.0 ± 0.30	10.7 ± 0.24	10.3 ± 0.29	9.9 ± 0.40	9.3 ± 0.14	9.3 ± 0.10	9.5 ± 0.38	10.2 ± 0.32	10.6 ± 0.24	-----
c-22	<0.001	5.3	-----	12.4 ± 0.93	15.9 ± 0.48	15.1 ± 0.39	16.0 ± 0.32	11.9 ± 0.42	11.4 ± 0.29	10.9 ± 0.39	10.7 ± 0.51	12.9 ± 0.41	-----
FA conc. % wet wt.	0.285	1.0	-----	1.7	1.2	1.5	1.2	1.2	1.1	0.7	1.0	1.5	-----

Appendix 7. Seasonal changes in the fatty acid composition of combined polar lipids in ovarian and somatic tissues of pike. Mean ± SE

Fatty Acid	p Value[c]	Seasonal[d] Range wt %	1987					1988					
			May	June[b] 6	July 6	August 7	Sept. 6	Jan. 6	March 7	May[e] 2	May[f] 4	June 8	Aug.
16:0	<0.001	1.6	-----	19.4[a] ± 0.25	19.5 ± 0.36	19.5 ± 0.22	19.0 ± 0.33	18.5 ± 0.13	18.3 ± 0.17	18.9 ± 0.14	17.9 ± 0.29	18.4 ± 0.17	-----
18:0	<0.001	2.1	-----	7.4 ± 0.12	7.2 ± 0.03	6.8 ± 0.05	6.9 ± 0.10	5.4 ± 0.04	5.4 ± 0.05	5.3 ± 0.02	6.7 ± 0.09	7.4 ± 0.11	-----
16:1n7	<0.001	4.5	-----	4.3 ± 0.31	4.1 ± 0.06	4.7 ± 0.27	5.4 ± 0.17	7.8 ± 0.12	8.6 ± 0.15	8.0 ± 0.08	5.0 ± 0.26	4.7 ± 0.25	-----
18:1n9	<0.001	2.9	-----	10.1 ± 0.14	9.6 ± 0.24	10.0 ± 0.28	10.0 ± 0.22	12.5 ± 0.29	12.2 ± 0.19	11.5 ± 0.25	9.7 ± 0.24	10.0 ± 0.13	-----
18:2n6	<0.001	0.6	-----	2.4 ± 0.07	2.1 ± 0.05	2.5 ± 0.11	2.4 ± 0.07	2.7 ± 0.05	2.6 ± 0.04	2.6 ± 0.11	2.6 ± 0.21	2.3 ± 0.08	-----
20:4n6	0.558	0.6	-----	7.8 ± 0.30	7.6 ± 0.31	7.3 ± 0.11	7.9 ± 0.17	7.6 ± 0.12	7.6 ± 0.10	7.8 ± 0.42	7.8 ± 0.38	7.7 ± 0.20	-----
22:5n6	0.002	0.4	-----	1.6 ± 0.04	1.9 ± 0.06	1.7 ± 0.05	1.8 ± 0.07	1.8 ± 0.02	1.7 ± 0.03	1.6 ± 0.12	2.0 ± 0.09	1.9 ± 0.05	-----
18:3n3	<0.001	0.9	-----	1.6 ± 0.05	1.5 ± 0.05	2.1 ± 0.13	1.8 ± 0.09	2.4 ± 0.04	2.4 ± 0.06	2.4 ± 0.11	2.1 ± 0.14	1.5 ± 0.05	-----
20:5n3	0.002	0.9	-----	7.0 ± 0.22	7.3 ± 0.11	7.7 ± 0.07	7.1 ± 0.09	7.3 ± 0.04	7.3 ± 0.07	7.1 ± 0.43	6.8 ± 0.34	6.9 ± 0.13	-----
22:5n3	0.056	0.3	-----	2.0 ± 0.07	2.0 ± 0.07	2.0 ± 0.05	2.0 ± 0.06	2.0 ± 0.05	2.1 ± 0.06	2.1 ± 0.15	2.3 ± 0.11	2.1 ± 0.06	-----
22:6n3	<0.001	5.6	-----	31.0 ± 0.11	32.2 ± 0.27	31.2 ± 0.70	31.2 ± 0.88	27.0 ± 0.56	26.9 ± 0.44	27.6 ± 1.03	32.5 ± 0.86	32.3 ± 0.36	-----
others	<0.001	0.6	-----	4.4 ± 0.08	4.2 ± 0.08	3.9 ± 0.03	3.8 ± 0.13	4.0 ± 0.06	3.8 ± 0.09	3.8 ± 0.10	3.8 ± 0.07	4.0 ± 0.06	-----
SFA	<0.001	2.9	-----	27.8 ± 0.25	27.5 ± 0.35	27.0 ± 0.26	26.6 ± 0.43	25.0 ± 0.13	24.9 ± 0.15	25.3 ± 0.15	25.5 ± 0.41	26.6 ± 0.24	-----
MUFA	<0.001	7.0	-----	14.5 ± 0.43	13.7 ± 0.23	14.7 ± 0.49	15.4 ± 0.35	20.3 ± 0.40	20.7 ± 0.28	19.5 ± 0.18	14.7 ± 0.49	14.6 ± 0.33	-----
PUFA	<0.001	5.4	-----	53.3 ± 0.37	54.6 ± 0.52	54.3 ± 0.68	54.3 ± 0.83	50.7 ± 0.46	50.6 ± 0.36	51.4 ± 0.13	56.0 ± 0.95	54.8 ± 0.39	-----
all n-6	0.201	0.9	-----	11.9 ± 0.30	11.6 ± 0.33	11.5 ± 0.08	12.1 ± 0.14	12.1 ± 0.11	12.0 ± 0.09	12.1 ± 0.43	12.4 ± 0.50	11.9 ± 0.15	-----
all n-3	<0.001	5.0	-----	41.5 ± 0.23	43.0 ± 0.38	42.8 ± 0.67	42.2 ± 0.87	38.6 ± 0.54	38.6 ± 0.44	39.3 ± 0.56	43.6 ± 0.66	42.9 ± 0.38	-----
c-16	<0.001	4.0	-----	23.7 ± 0.22	23.6 ± 0.32	24.3 ± 0.35	24.4 ± 0.45	26.3 ± 0.23	26.9 ± 0.24	26.9 ± 0.22	22.9 ± 0.52	23.1 ± 0.29	-----
c-18	<0.001	2.5	-----	21.5 ± 0.30	20.5 ± 0.22	21.3 ± 0.47	21.1 ± 0.35	23.0 ± 0.30	22.5 ± 0.19	21.8 ± 0.01	21.1 ± 0.34	21.1 ± 0.24	-----
c-20	0.968	0.5	-----	14.8 ± 0.43	14.9 ± 0.35	14.9 ± 0.17	15.0 ± 0.17	14.9 ± 0.14	14.9 ± 0.10	14.9 ± 0.85	14.5 ± 0.71	14.7 ± 0.16	-----
c-22	<0.001	6.1	-----	34.5 ± 0.11	36.1 ± 0.29	34.9 ± 0.75	35.0 ± 0.91	30.8 ± 0.56	30.7 ± 0.45	31.4 ± 0.76	36.8 ± 0.77	36.3 ± 0.44	-----
FA conc. % wet wt.	<0.001	0.64	-----	0.34	0.33	0.37	0.50	0.82	0.97	0.82	0.41	0.36	-----

Appendix 8. Seasonal changes in the fatty acid composition of combined total lipids in somatic tissues of pike.

Fatty Acid	p value[c]	Seasonal[d] Range wt %		1987				1988				
			May	June[b] 5	July 6	August 7	Sept. 4	Jan. 6	March 7	May 7	June 7	Aug. 6
16:0	<0.001	2.1	-----	15.8[a]	15.1	14.4	14.3	14.2	13.7	14.3	14.0	14.4
				± 0.51	± 0.03	± 0.12	± 0.17	± 0.15	± 0.17	± 0.29	± 0.16	± 0.26
18:0	<0.001	0.6	-----	6.5	6.4	5.9	6.4	6.0	6.0	6.0	6.2	6.2
				± 0.10	± 0.07	± 0.05	± 0.04	± 0.03	± 0.05	± 0.07	± 0.13	± 0.11
16:1n7	<0.001	3.2	-----	12.9	12.3	13.4	12.8	14.6	15.5	15.0	15.4	15.3
				± 0.31	± 0.53	± 0.24	± 0.60	± 0.28	± 0.27	± 0.86	± 0.32	± 0.27
18:1n9	0.015	3.0	-----	18.7	16.8	16.6	16.1	17.1	16.7	16.0	19.0	17.3
				± 1.11	± 0.90	± 0.32	± 0.17	± 0.42	± 0.49	± 0.54	± 0.75	± 0.27
18:2n6	0.002	0.9	-----	5.4	5.2	5.8	5.5	5.4	5.2	5.2	5.2	6.1
				± 0.07	± 0.13	± 0.17	± 0.31	± 0.22	± 0.18	± 0.10	± 0.17	± 0.18
20:4n6	0.270	0.7	-----	5.2	5.2	4.7	5.1	5.0	5.2	5.4	5.0	5.0
				± 0.18	± 0.22	± 0.11	± 0.26	± 0.16	± 0.11	± 0.27	± 0.11	± 0.13
22:5n6	0.017	0.4	-----	1.1	1.4	1.3	1.5	1.3	1.4	1.4	1.3	1.4
				± 0.09	± 0.08	± 0.03	± 0.06	± 0.06	± 0.04	± 0.04	± 0.06	± 0.03
18:3n3	<0.001	1.4	-----	4.9	4.9	6.2	5.2	5.9	5.8	5.4	4.9	4.8
				± 0.16	± 0.20	± 0.32	± 0.30	± 0.37	± 0.23	± 0.22	± 0.17	± 0.13
20:5n3	0.107	0.7	-----	6.7	6.6	6.5	6.0	6.2	6.5	6.4	6.4	6.3
				± 0.23	± 0.09	± 0.18	± 0.17	± 0.07	± 0.11	± 0.10	± 0.16	± 0.11
22:5n3	<0.001	0.4	-----	1.8	2.1	1.9	2.1	1.8	1.8	1.7	2.0	2.1
				± 0.04	± 0.04	± 0.04	± 0.02	± 0.08	± 0.04	± 0.03	± 0.04	± 0.03
22:6n3	0.067	4.5	-----	13.7	17.2	16.0	18.2	15.4	15.4	16.2	14.3	14.9
				± 1.24	± 1.19	± 0.58	± 1.30	± 0.88	± 0.69	± 1.20	± 0.54	± 0.64
others	0.027	0.9	-----	7.1	6.7	7.0	6.6	6.7	6.7	6.8	6.2	6.2
				± 0.25	± 0.10	± 0.14	± 0.35	± 0.11	± 0.15	± 0.23	± 0.23	± 0.15
SFA	<0.001	2.6	-----	22.5	21.6	20.4	20.8	20.5	19.9	20.4	20.4	20.8
				± 0.56	± 0.11	± 0.15	± 0.18	± 0.18	± 0.22	± 0.37	± 0.25	± 0.38
MUFA	0.003	5.4	-----	31.5	29.1	30.0	28.9	31.8	32.2	31.0	34.3	32.5
				± 1.31	± 1.32	± 0.51	± 0.76	± 0.55	± 0.58	± 1.35	± 0.86	± 0.43
PUFA	0.011	4.7	-----	38.9	42.6	42.5	43.6	41.0	41.2	41.8	39.1	40.4
				± 1.48	± 1.25	± 0.49	± 0.93	± 0.59	± 0.54	± 1.28	± 0.54	± 0.46
all n-6	0.014	1.1	-----	11.7	11.8	11.9	12.1	11.8	11.7	12.1	11.4	12.5
				± 0.22	± 0.18	± 0.07	± 0.16	± 0.07	± 0.10	± 0.33	± 0.14	± 0.08
all n-3	0.004	4.3	-----	27.2	30.9	30.6	31.5	29.2	29.5	29.7	27.6	28.0
				± 1.28	1.08	0.49	0.98	0.62	0.57	0.99	0.42	0.52
c-16	<0.001	2.6	-----	28.7	27.3	27.8	27.1	28.9	29.1	29.2	29.4	29.7
				± 0.65	± 0.51	± 0.19	± 0.45	± 0.26	± 0.15	± 0.63	± 0.22	± 0.32
c-18	0.158	2.8	-----	35.4	33.3	34.6	33.2	34.4	33.7	32.6	35.3	34.4
				± 1.14	± 0.99	± 0.61	± 0.77	± 0.92	± 0.79	± 0.67	± 0.58	± 0.47
c-20	0.205	0.8	-----	11.9	11.8	11.2	11.1	11.2	11.7	11.9	11.4	11.3
				± 0.27	± 0.26	± 0.25	± 0.38	± 0.20	± 0.21	± 0.31	± 0.20	± 0.19
c-22	0.059	5.1	-----	16.7	20.7	19.2	21.8	18.5	18.5	19.3	17.5	18.3
				± 1.34	± 1.28	± 0.63	± 1.34	± 0.99	± 0.75	± 1.24	± 0.61	± 0.66
FA conc. % wet wt.	0.596	0.50	-----	1.87	1.56	1.87	1.68	1.67	1.57	1.42	1.92	1.64

Appendix 9. Seasonal changes in the fatty acid composition of combined total lipids in ovarian and somatic tissues of pike.

Fatty Acid	p Value[c]	Seasonal[d] Range wt %	1987					1988					
			May	June[b] 5	July 6	August 7	Sept. 4	Jan. 6	March 7	May[e] 2	May[f] 4	June 7	Aug.
16:0	<0.001	1.8	-----	15.8[a]	15.1	14.4	14.5	14.9	14.8	15.7	14.4	14.0	-----
				± 0.51	± 0.04	± 0.12	± 0.21	± 0.17	± 0.18	± 0.24	± 0.34	± 0.16	
18:0	<0.001	0.9	-----	6.5	6.4	6.0	6.4	5.8	5.8	5.6	6.0	6.2	-----
				± 0.10	± 0.07	± 0.05	± 0.04	± 0.02	± 0.05	± 0.04	± 0.09	± 0.13	
16:1n7	<0.001	3.1	-----	12.9	12.3	13.4	12.7	13.9	14.3	13.2	14.9	15.4	-----
				± 0.31	± 0.53	± 0.24	± 0.60	± 0.23	± 0.20	± 0.66	± 1.29	± 0.33	
18:1n9	0.031	2.9	-----	18.6	16.8	16.6	16.0	17.8	17.5	16.7	16.4	18.9	-----
				± 1.11	± 0.89	± 0.33	± 0.15	± 0.39	± 0.35	± 0.28	± 0.80	± 0.75	
18:2n6	<0.001	1.4	-----	5.4	5.2	5.8	5.4	4.9	4.6	4.4	5.1	5.2	-----
				± 0.07	± 0.13	± 0.17	± 0.31	± 0.18	± 0.13	± 0.05	± 0.10	± 0.17	
20:4n6	0.085	1.3	-----	5.2	5.2	4.8	5.3	5.4	5.6	6.1	5.4	5.0	-----
				± 0.19	± 0.23	± 0.12	± 0.27	± 0.12	± 0.09	± 0.04	± 0.45	± 0.11	
22:5n6	0.017	0.4	-----	1.1	1.4	1.3	1.5	1.3	1.3	1.3	1.4	1.3	-----
				± 0.09	± 0.08	± 0.03	± 0.06	± 0.04	± 0.02	± 0.04	± 0.05	± 0.06	
18:3n3	0.003	1.9	-----	4.9	4.9	6.1	5.0	5.1	4.7	4.2	5.2	4.9	-----
				± 0.16	± 0.20	± 0.32	± 0.31	± 0.29	± 0.19	± 0.13	± 0.27	± 0.17	
20:5n3	0.151	0.6	-----	6.7	6.6	6.5	6.1	6.2	6.3	6.3	6.3	6.4	-----
				± 0.23	± 0.09	± 0.18	± 0.16	± 0.06	± 0.07	± 0.35	± 0.12	± 0.16	
22:5n3	<0.001	0.4	-----	1.8	2.1	1.9	2.1	1.7	1.8	1.7	1.7	2.0	-----
				± 0.04	± 0.04	± 0.04	± 0.02	± 0.06	± 0.04	± 0.08	± 0.05	± 0.04	
22:6n3	0.018	5.3	-----	13.7	17.2	16.0	18.4	16.6	17.3	19.0	16.1	14.3	-----
				± 1.23	± 1.19	± 0.57	± 1.26	± 0.63	± 0.46	± 1.63	± 1.75	± 0.54	
others	<0.001	2.0	-----	7.1	6.7	7.0	6.4	5.9	5.5	5.1	6.7	6.2	-----
				± 0.25	± 0.10	± 0.14	± 0.36	± 0.15	± 0.16	± 0.44	± 0.36	± 0.23	
SFA	<0.001	2.1	-----	22.5	21.7	20.5	21.1	21.2	21.2	21.9	20.7	20.4	-----
				± 0.56	± 0.12	± 0.16	± 0.22	± 0.20	± 0.23	± 0.33	± 0.43	± 0.25	
MUFA	0.003	5.6	-----	31.5	29.0	30.0	28.7	31.7	31.9	29.9	31.3	34.3	-----
				± 1.31	± 1.32	± 0.51	± 0.74	± 0.41	± 0.39	± 0.93	± 2.01	± 0.86	
PUFA	0.009	4.8	-----	38.9	42.6	42.5	43.7	41.2	41.5	43.1	41.3	39.1	-----
				± 1.47	± 1.24	± 0.48	± 0.88	± 0.43	± 0.37	± 1.05	± 2.03	± 0.54	
all n-6	0.189	0.7	-----	11.8	11.8	11.9	12.2	11.7	11.5	11.8	12.0	11.5	-----
				± 0.22	± 0.19	± 0.06	± 0.15	± 0.05	± 0.06	± 0.03	± 0.59	± 0.14	
all n-3	0.004	4.4	-----	27.2	30.8	30.6	31.6	29.6	30.0	31.3	29.4	27.6	-----
				± 1.27	± 1.07	± 0.49	± 0.93	± 0.46	± 0.39	± 1.07	± 1.49	± 0.42	
c-16	<0.001	2.2	-----	28.7	27.4	27.8	27.2	28.8	29.2	28.9	29.3	29.4	-----
				± 0.65	± 0.50	± 0.18	± 0.41	± 0.17	± 0.07	± 0.41	± 1.03	± 0.22	
c-18	0.050	4.5	-----	35.4	33.3	34.5	32.8	33.6	32.6	30.9	32.7	35.3	-----
				± 1.13	± 0.99	± 0.61	± 0.76	± 0.69	± 0.53	± 0.32	± 0.89	± 0.58	
c-20	0.475	1.1	-----	11.9	11.8	11.3	11.4	11.6	11.9	12.4	11.8	11.4	-----
				± 0.28	± 0.27	± 0.25	± 0.38	± 0.15	± 0.14	± 0.39	± 0.49	± 0.20	
c-22	0.020	5.4	-----	16.7	20.7	19.3	21.9	19.7	20.3	22.1	19.3	17.5	-----
				± 1.34	± 1.27	± 0.62	± 1.29	± 0.71	± 0.50	± 1.51	± 1.83	± 0.61	
FA conc. % wet wt.	0.343	0.66	-----	1.86	1.55	1.86	1.71	2.01	2.10	1.53	1.44	1.91	-----

Appendix 10. Seasonal changes in the content (g / kg carcass weight) of major fatty acid groups in various lipid compartments of female northern pike.

Fatty Acid	p Value[c]	1987 May	June	July	August	Sept.	1988 Jan.	March	May[e]	May[f]	June	Aug.
						Ovary Neutral Lipids						
			(6)[b]	(6)	(7)	(7)	(7)	(7)	(2)	(4)	(8)	
SFA	<0.001	----	0.001[a] ± 0.0002	0.002 ± 0.0003	0.007 ± 0.0006	0.041 ± 0.0095	0.209 ± 0.0266	0.329 ± 0.0312	0.324 ± 0.0054	0.003 ± 0.0002	0.002 ± 0.0001	----
MUFA	<0.001	----	0.002 ± 0.0003	0.003 ± 0.0005	0.011 ± 0.0010	0.080 ± 0.0215	0.627 ± 0.0803	0.970 ± 0.0914	0.912 ± 0.0216	0.006 ± 0.0006	0.002 ± 0.0002	----
PUFA	<0.001	----	0.002 ± 0.0003	0.003 ± 0.0007	0.017 ± 0.0021	0.087 ± 0.0137	0.366 ± 0.0401	0.582 ± 0.0459	0.597 ± 0.0328	0.006 ± 0.0002	0.003 ± 0.0003	----
n-3	<0.001	----	0.002 ± 0.0002	0.002 ± 0.0005	0.013 ± 0.0016	0.061 ± 0.0083	0.240 ± 0.0249	0.387 ± 0.0298	0.395 ± 0.0196	0.004 ± 0.0002	0.002 ± 0.0002	----
n-6	<0.001	----	0.001 ± 0.0001	0.001 ± 0.0002	0.004 ± 0.0005	0.027 ± 0.0056	0.125 ± 0.0155	0.195 ± 0.0162	0.203 ± 0.0132	0.002 ± 0.0001	0.001 ± 0.0001	----
						Ovary Polar Lipids						
		(4)	(7)	(6)	(7)	(7)	(7)	(7)	(2)	(4)	(8)	
SFA	<0.001	0.016 ± 0.0034	0.007 ± 0.0004	0.011 ± 0.0015	0.029 ± 0.0019	0.141 ± 0.0307	0.790 ± 0.1051	1.173 ± 0.1044	1.089 ± 0.0333	0.017 ± 0.0009	0.008 ± 0.0006	----
MUFA	<0.001	0.012 ± 0.0025	0.005 ± 0.0003	0.008 ± 0.0010	0.021 ± 0.0014	0.103 ± 0.0218	0.738 ± 0.0943	1.084 ± 0.1014	0.973 ± 0.0363	0.014 ± 0.0006	0.005 ± 0.0004	----
PUFA	<0.001	0.024 ± 0.0050	0.010 ± 0.0006	0.014 ± 0.0020	0.042 ± 0.0030	0.233 ± 0.0489	1.443 ± 0.1828	2.170 ± 0.1916	2.013 ± 0.0380	0.027 ± 0.0016	0.011 ± 0.0007	----
n-3	<0.001	0.014 ± 0.0027	0.006 ± 0.0004	0.009 ± 0.0013	0.029 ± 0.0021	0.168 ± 0.0360	1.073 ± 0.1365	1.633 ± 0.1417	1.529 ± 0.0069	0.017 ± 0.0011	0.007 ± 0.0005	----
n-6	<0.001	0.010 ± 0.0023	0.004 ± 0.0002	0.005 ± 0.0007	0.013 ± 0.0009	0.065 ± 0.0129	0.371 ± 0.0463	0.537 ± 0.0501	0.484 ± 0.0311	0.010 ± 0.0006	0.004 ± 0.0003	----

Fatty Acid	p Value	1987 May	June	July	August	Sept.	1988 Jan.	March	May	June	Aug.
						Liver Neutral Lipids					
			(7)	(6)	(7)	(5)	(7)	(7)	(7)	(8)	(6)
SFA	<0.001	----	0.261 ± 0.0920	0.107 ± 0.0222	0.085 ± 0.0108	0.073 ± 0.0230	0.023 ± 0.0030	0.026 ± 0.0045	0.051 ± 0.0289	0.113 ± 0.0199	0.107 ± 0.0096
MUFA	0.002	----	0.537 ± 0.1878	0.228 ± 0.0454	0.200 ± 0.0267	0.185 ± 0.0545	0.063 ± 0.0093	0.075 ± 0.0166	0.124 ± 0.0708	0.297 ± 0.0599	0.256 ± 0.0181
PUFA	<0.001	----	0.269 ± 0.0514	0.229 ± 0.0376	0.197 ± 0.0316	0.123 ± 0.0373	0.033 ± 0.0047	0.035 ± 0.0039	0.054 ± 0.0236	0.224 ± 0.0368	0.235 ± 0.0245
n-3	<0.001	----	0.174 ± 0.0325	0.152 ± 0.0254	0.123 ± 0.0206	0.066 ± 0.0206	0.020 ± 0.0027	0.020 ± 0.0019	0.033 ± 0.0152	0.143 ± 0.0233	0.143 ± 0.0171
n-6	<0.001	----	0.095 ± 0.0191	0.077 ± 0.0123	0.074 ± 0.0111	0.056 ± 0.0169	0.013 ± 0.0020	0.015 ± 0.0021	0.021 ± 0.0084	0.081 ± 0.0135	0.092 ± 0.0081

Appendix 10. cont... Seasonal changes in the content (g / kg carcass weight) of major fatty acid groups in various lipid compartments of female northern pike.

Fatty Acid	p Value^c	1987 May	1987 June	1987 July	1987 August	1987 Sept.	1988 Jan.	1988 March	1988 May	1988 June	1988 Aug.
						Liver Polar Lipids					
		(4)^b	(6)	(6)	(7)	(7)	(7)	(7)	(7)	(8)	(6)
SFA	<0.001	0.054^a	0.041	0.042	0.048	0.077	0.139	0.117	0.068	0.043	0.043
		± 0.0042	± 0.0011	± 0.0022	± 0.0020	± 0.0056	± 0.0073	± 0.0046	± 0.0028	± 0.0022	± 0.0038
MUFA	<0.001	0.037	0.023	0.024	0.032	0.056	0.129	0.100	0.046	0.027	0.026
		± 0.0021	± 0.0007	± 0.0013	± 0.0013	± 0.0034	± 0.0066	± 0.0035	± 0.0017	± 0.0011	± 0.0018
PUFA	<0.001	0.098	0.071	0.072	0.090	0.140	0.258	0.222	0.127	0.077	0.076
		± 0.0044	± 0.0021	± 0.0042	± 0.0033	± 0.0068	± 0.0151	± 0.0095	± 0.0031	± 0.0021	± 0.0053
n-3	<0.001	0.075	0.054	0.053	0.068	0.103	0.192	0.166	0.097	0.056	0.055
		± 0.0033	± 0.0018	± 0.0031	± 0.0025	± 0.0046	± 0.0114	± 0.0072	± 0.0025	± 0.0015	± 0.0040
n-6	<0.001	0.023	0.017	0.019	0.022	0.037	0.067	0.056	0.030	0.021	0.020
		± 0.0012	± 0.0004	± 0.0012	± 0.0009	± 0.0022	± 0.0037	± 0.0025	± 0.0007	± 0.0007	± 0.0014
						Muscle Neutral Lipids					
		(5)	(6)	(6)	(7)	(6)	(6)	(7)	(7)	(7)	(6)
SFA	0.213	0.643	0.537	0.473	0.686	0.771	0.475	0.476	0.333	0.479	0.448
		± 0.1135	± 0.1067	± 0.1015	± 0.1723	± 0.2225	± 0.0402	± 0.0647	± 0.0483	± 0.0538	± 0.0221
MUFA	0.253	1.187	0.824	0.720	1.168	1.348	0.878	0.964	0.680	0.918	0.838
		± 0.2118	± 0.1633	± 0.1413	± 0.2611	± 0.3987	± 0.0724	± 0.1224	± 0.0955	± 0.1124	± 0.0422
PUFA	0.070	1.215	0.909	0.859	1.363	1.571	0.859	0.854	0.601	0.851	0.855
		± 0.2512	± 0.1738	± 0.1715	± 0.2974	± 0.4773	± 0.0732	± 0.1137	± 0.0741	± 0.1155	± 0.0495
n-3	0.055	0.823	0.610	0.600	0.950	1.085	0.581	0.577	0.404	0.578	0.571
		± 0.1596	± 0.1194	± 0.1205	± 0.2065	± 0.3290	± 0.0522	± 0.0793	± 0.0560	± 0.0817	± 0.0325
n-6	0.115	0.393	0.299	0.259	0.412	0.485	0.277	0.278	0.197	0.273	0.284
		± 0.0917	± 0.0547	± 0.0511	± 0.0911	± 0.1484	± 0.0212	± 0.0348	± 0.0182	± 0.0341	± 0.0176
						Muscle Polar Lipids					
		(5)	(7)	(6)	(7)	(6)	(6)	(7)	(7)	(8)	(6)
SFA	<0.001	0.461	0.489	0.462	0.493	0.565	0.532	0.510	0.508	0.488	0.470
		± 0.0367	± 0.0243	± 0.0190	± 0.0155	± 0.0125	± 0.0046	± 0.0086	± 0.0054	± 0.0068	± 0.0066
MUFA	<0.001	0.262	0.252	0.222	0.256	0.289	0.317	0.315	0.274	0.261	0.224
		± 0.0240	± 0.0212	± 0.0085	± 0.0158	± 0.0077	± 0.0062	± 0.0136	± 0.0061	± 0.0063	± 0.0088
PUFA	<0.001	1.002	0.943	0.940	1.018	1.230	1.233	1.250	1.196	1.029	0.934
		± 0.0575	± 0.0504	± 0.0463	± 0.0411	± 0.0519	± 0.0147	± 0.0231	± 0.0301	± 0.0203	± 0.0036
n-3	<0.001	0.783	0.740	0.747	0.812	0.975	0.969	0.980	0.937	0.814	0.730
		± 0.0504	± 0.0421	± 0.0369	± 0.0334	± 0.0424	± 0.0169	± 0.0185	± 0.0236	± 0.0175	± 0.0092
n-6	<0.001	0.219	0.203	0.192	0.207	0.255	0.264	0.270	0.259	0.216	0.204
		± 0.0086	± 0.0091	± 0.0108	± 0.0084	± 0.0113	± 0.0075	± 0.0099	± 0.0098	± 0.0040	± 0.0070

Appendix 10. cont... Seasonal changes in the content (g / kg carcass weight) of major fatty acid groups in various lipid compartments of female northern pike.

Fatty Acid	P Value[c]		1987				1988				
		May	June	July	August	Sept.	Jan.	March	May	June	Aug.
					Adipopancreatic Tissue Neutral Lipids						
			(7)[b]	(6)	(7)	(7)	(7)	(7)	(7)	(8)	(6)
SFA	0.380	----	1.201[a]	0.823	0.851	0.641	0.873	0.690	0.676	1.005	0.861
			± 0.2774	± 0.1933	± 0.1342	± 0.0533	± 0.1566	± 0.1038	± 0.1742	± 0.1739	± 0.1756
MUFA	0.564	----	1.921	1.451	1.567	1.165	1.794	1.521	1.493	2.114	1.708
			± 0.3957	± 0.3494	± 0.2419	± 0.1129	± 0.2893	± 0.2182	± 0.3822	± 0.3800	± 0.3221
PUFA	0.689	----	1.959	1.607	1.816	1.325	1.656	1.381	1.323	1.903	1.646
			± 0.3827	± 0.3451	± 0.2778	± 0.1230	± 0.2470	± 0.1943	± 0.3479	± 0.3326	± 0.2989
n-3	0.642	----	1.330	1.122	1.269	0.913	1.107	0.929	0.872	1.294	1.087
			± 0.2609	± 0.2424	± 0.1950	± 0.0865	± 0.1597	± 0.1322	± 0.2375	± 0.2273	± 0.1946
n-6	0.728	----	0.630	0.485	0.547	0.412	0.549	0.452	0.451	0.610	0.559
			± 0.1236	± 0.1030	± 0.0828	± 0.0369	± 0.0873	± 0.0627	± 0.1110	± 0.1056	± 0.1053
					Adipopancreatic Tissue Polar Lipids						
			(7)	(6)	(7)	(7)	(7)	(7)	(7)	(8)	(6)
SFA	<0.001	----	0.011	0.008	0.009	0.010	0.012	0.015	0.014	0.011	0.009
			± 0.0016	± 0.0006	± 0.0005	± 0.0010	± 0.0011	± 0.0018	± 0.0013	± 0.0005	± 0.0005
MUFA	<0.001	----	0.008	0.006	0.007	0.008	0.013	0.016	0.013	0.009	0.007
			± 0.0010	± 0.0002	± 0.0003	± 0.0008	± 0.0010	± 0.0020	± 0.0012	± 0.0004	± 0.0004
PUFA	<0.001	----	0.018	0.012	0.016	0.017	0.024	0.030	0.026	0.017	0.015
			± 0.0027	± 0.0011	± 0.0009	± 0.0019	± 0.0021	± 0.0039	± 0.0025	± 0.0010	± 0.0009
n-3	<0.001	----	0.012	0.008	0.011	0.011	0.016	0.020	0.018	0.011	0.010
			± 0.0018	± 0.0007	± 0.0006	± 0.0014	± 0.0014	± 0.0026	± 0.0017	± 0.0007	± 0.0006
n-6	<0.001	----	0.006	0.004	0.005	0.006	0.007	0.010	0.008	0.006	0.005
			± 0.0009	± 0.0004	± 0.0003	± 0.0006	± 0.0007	± 0.0013	± 0.0008	± 0.0004	± 0.0003

Appendix 10. cont... Seasonal changes in the content (g / kg carcass weight) of major fatty acid groups in various lipid compartments of female northern pike.

		1987					1988				
Fatty Acid	p Value[c]	May	June	July	August	Sept.	Jan.	March	May	June	Aug.
						Somatic Tissue Neutral Lipids					
			(6)[b]	(6)	(7)	(4)	(6)	(7)	(7)	(7)	(6)
SFA	0.085	----	2.137[a]	1.403	1.621	1.371	1.345	1.192	1.061	1.680	1.416
		±	0.3602	± 0.2414	± 0.2362	± 0.3357	± 0.1848	± 0.1334	± 0.2197	± 0.1900	± 0.1859
MUFA	0.348	----	3.506	2.399	2.935	2.478	2.701	2.560	2.297	3.518	2.802
		±	0.5378	± 0.4217	± 0.4079	± 0.5806	± 0.3439	± 0.2724	± 0.4753	± 0.4348	± 0.3459
PUFA	0.186	----	3.269	2.695	3.376	2.808	2.513	2.271	1.978	3.136	2.737
		±	0.3988	± 0.4242	± 0.4573	± 0.6962	± 0.3076	± 0.2405	± 0.4004	± 0.3565	± 0.3333
n-3	0.138	----	2.195	1.875	2.342	1.920	1.688	1.526	1.310	2.125	1.802
		±	0.2709	± 0.2969	± 0.3169	± 0.4711	± 0.2014	± 0.1595	± 0.2769	± 0.2400	± 0.2193
n-6	0.283	----	1.075	0.821	1.034	0.887	0.825	0.745	0.669	1.011	0.935
		±	0.1303	± 0.1276	± 0.1405	± 0.2252	± 0.1065	± 0.0814	± 0.1240	± 0.1166	± 0.1148
						Somatic Tissue Polar Lipids					
			(6)	(6)	(7)	(6)	(6)	(7)	(7)	(8)	(6)
SFA	<0.001	----	0.543	0.511	0.550	0.654	0.680	0.641	0.590	0.542	0.521
		±	0.0295	± 0.0190	± 0.0164	± 0.0175	± 0.0093	± 0.0106	± 0.0067	± 0.0072	± 0.0084
MUFA	<0.001	----	0.283	0.251	0.294	0.355	0.458	0.431	0.334	0.297	0.257
		±	0.0254	± 0.0086	± 0.0167	± 0.0108	± 0.0127	± 0.0156	± 0.0076	± 0.0059	± 0.0096
PUFA	<0.001	----	1.045	1.024	1.124	1.389	1.508	1.502	1.349	1.124	1.025
		±	0.0594	± 0.0497	± 0.0426	± 0.0521	± 0.0186	± 0.0288	± 0.0284	± 0.0212	± 0.0064
n-3	<0.001	----	0.815	0.809	0.890	1.091	1.172	1.167	1.052	0.881	0.795
		±	0.0497	± 0.0390	± 0.0346	± 0.0418	± 0.0126	± 0.0210	± 0.0228	± 0.0181	± 0.0105
n-6	<0.001	----	0.230	0.215	0.234	0.297	0.337	0.336	0.297	0.242	0.230
		±	0.0104	± 0.0120	± 0.0088	± 0.0125	± 0.0115	± 0.0120	± 0.0090	± 0.0043	± 0.0071
						Somatic Tissue Total Lipids					
			(5)	(6)	(7)	(4)	(6)	(7)	(7)	(7)	(6)
SFA	0.442	----	2.417	1.914	2.171	2.001	2.025	1.833	1.650	2.225	1.937
			± 0.3494	± 0.2301	± 0.2427	± 0.3313	± 0.1897	± 0.1416	± 0.2228	± 0.1969	± 0.1865
MUFA	0.568	----	3.427	2.650	3.229	2.820	3.159	2.991	2.630	3.810	3.059
			± 0.5202	± 0.4169	± 0.4097	± 0.5782	± 0.3481	± 0.2830	± 0.4820	± 0.4374	± 0.3471
PUFA	0.570	----	4.1013	3.720	4.500	4.160	4.022	3.773	3.328	4.266	3.762
			± 0.4844	± 0.3809	± 0.4854	± 0.6267	± 0.3050	± 0.2564	± 0.4001	± 0.3715	± 0.3297
n-3	0.466	----	2.856	2.684	3.232	2.991	2.860	2.693	2.362	3.012	2.597
			± 0.3344	± 0.2655	± 0.3403	± 0.4104	± 0.1949	± 0.1682	± 0.2807	± 0.2532	± 0.2125
n-6	0.682	----	1.246	1.036	1.268	1.169	1.162	1.080	0.966	1.254	1.165
			± 0.1531	± 0.1162	± 0.1457	± 0.2164	± 0.1106	± 0.0889	± 0.1200	± 0.1184	± 0.1186

Appendix 10. cont... Seasonal changes in the content (g / kg carcass weight) of major fatty acid groups in various lipid compartments of female northern pike.

		1987					1988					
Fatty Acid	P Value^c	May	June	July	August	Sept.	Jan.	March	May^e	May^f	June	Aug.
						All Tissues Combined - Neutral Lipids						
			(6)^b	(6)	(7)	(4)	(6)	(7)	(2)	(4)	(7)	
SFA	0.315	----	2.139^a	1.405	1.628	1.404	1.540	1.521	1.002	1.122	1.682	----
			± 0.3602	± 0.2415	± 0.2361	± 0.3339	± 0.2035	± 0.1474	± 0.2057	± 0.3353	± 0.1900	
MUFA	0.343	----	3.508	2.401	2.946	2.538	3.290	3.529	2.374	2.400	3.520	----
			± 0.5378	± 0.4218	± 0.4079	± 0.5793	± 0.3950	± 0.3202	± 0.4384	± 0.7069	± 0.4348	
PUFA	0.571	----	3.272	2.699	3.392	2.881	2.862	2.853	1.861	2.049	3.138	----
			± 0.3987	± 0.4243	± 0.4572	± 0.6958	± 0.3396	± 0.2578	± 0.3427	± 0.5800	± 0.3565	
n-3	0.520	----	2.196	1.877	2.355	1.972	1.920	1.913	1.219	1.364	2.127	----
			± 0.2708	± 0.2970	± 0.3169	± 0.4706	± 0.2220	± 0.1704	± 0.2396	± 0.4091	± 0.2400	
n-6	0.623	----	1.075	0.822	1.038	0.909	0.943	0.940	0.642	0.685	1.011	----
			± 0.1303	± 0.1276	± 0.1405	± 0.2252	± 0.1179	± 0.0878	± 0.1032	± 0.1713	± 0.1166	
						All Tissues Combined - Polar Lipids						
			(6)	(6)	(7)	(6)	(6)	(7)	(2)	(4)	(8)	
SFA	<0.001	----	0.550	0.522	0.579	0.806	1.422	1.814	1.667	0.612	0.550	----
			± 0.0295	± 0.0185	± 0.0167	± 0.0489	± 0.1158	± 0.1101	± 0.0141	± 0.0072	± 0.0072	
MUFA	<0.001	----	0.288	0.259	0.315	0.466	1.159	1.515	1.287	0.353	0.303	----
			± 0.0254	± 0.0083	± 0.0173	± 0.0318	± 0.1110	± 0.1097	± 0.0301	± 0.0094	± 0.0060	
PUFA	<0.001	----	1.055	1.039	1.167	1.639	2.868	3.672	3.380	1.349	1.134	----
			± 0.0594	± 0.0497	± 0.0427	± 0.0829	± 0.2048	± 0.2028	± 0.0400	± 0.0452	± 0.0211	
n-3	<0.001	----	0.821	0.818	0.919	1.272	2.182	2.800	2.583	1.051	0.888	----
			± 0.0498	± 0.0389	± 0.0347	± 0.0614	± 0.1451	± 0.1448	± 0.0002	± 0.0352	± 0.0181	
n-6	<0.001	----	0.234	0.220	0.247	0.367	0.686	0.873	0.797	0.298	0.246	----
			± 0.0104	± 0.0122	± 0.0089	± 0.0229	± 0.0599	± 0.0585	± 0.0398	± 0.0144	± 0.0044	
						All Tissues Combined - Total Lipids						
			(5)	(6)	(7)	(4)	(6)	(7)	(2)	(4)	(7)	
SFA	0.002	----	2.426	1.927	2.207	2.145	2.962	3.335	2.669	1.734	2.234	----
			± 0.3493	± 0.2296	± 0.2426	± 0.3331	± 0.2963	± 0.2260	± 0.2199	± 0.3407	± 0.1968	
MUFA	0.008	----	3.434	2.660	3.261	2.963	4.449	5.045	3.661	2.753	3.818	----
			± 0.5203	± 0.4166	± 0.4097	± 0.5780	± 0.4759	± 0.3932	± 0.4684	± 0.7162	± 0.4373	
PUFA	<0.001	----	4.114	3.737	4.559	4.422	5.730	6.525	5.240	3.397	4.279	----
			± 0.4845	± 0.3800	± 0.4855	± 0.6324	± 0.4806	± 0.4018	± 0.3827	± 0.5684	± 0.3715	
n-3	<0.001	----	2.863	2.695	3.274	3.178	4.101	4.713	3.802	2.414	3.020	----
			± 0.3345	± 0.2649	± 0.3404	± 0.4146	± 0.3212	± 0.2754	± 0.2398	± 0.4068	± 0.2532	
n-6	0.003	----	1.250	1.042	1.285	1.244	1.629	1.812	1.439	0.983	1.259	----
			± 0.1530	± 0.1159	± 0.1456	± 0.2179	± 0.1597	± 0.1274	± 0.1429	± 0.1623	± 0.1184	